The efficacy of reintroducing the New Zealand falcon into the vineyards of Marlborough for pest control and falcon conservation

A thesis submitted in partial fulfilment of the requirements for the

DEGREE OF

DOCTOR OF PHILOSOPHY IN ZOOLOGY

at the

UNIVERSITY OF CANTERBURY

by

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UNIVERSITY OF CANTERBURY

Christchurch, New Zealand

2012

Dedicated to Poppop, who has taught me to love to learn.

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ABSTRACT

In our ever more populated world, the rapid expansion and intensification of agriculture is driving worldwide biodiversity loss, and the interactions between production landscapes and wildlife conservation are becoming increasingly important. Farming systems depend on ecosystem services such as biological control, while conservationists are calling for the establishment of conservation initiatives in non-preserve landscapes. Despite this, the goals of agriculture and the goals of predator-conservation are rarely mutual. Here, I demonstrate one of the first examples of a mutually beneficial scenario between agriculture and predator conservation. I used, as a case study, a reintroduction project that translocated individuals of the threatened New Zealand falcon (*Falco novaeseelandiae*) from the hills of Marlborough into vineyards, to determine if predators can survive within an agricultural landscape while simultaneously providing that landscape with biological control services.

Examples of vertebrates providing biological control to agriculture are rare. I show that the presence of falcons in vineyards caused an economically important reduction in grape damage worth over US $230/ ha. Falcon presence caused a 78- 83% reduction in the number of introduced European pest birds, which resulted in a 95% reduction in the damage caused by these species. Falcon presence did not cause a reduction in the abundance of the native silvereye (*Zosterops lateralis*), but did halve the damage caused by this species.

To assess the conservation value of the falcon translocations, I used remote videography, direct observations and prey analysis to measure the behavioural changes associated with the relocation of falcons from their natural habitat in the hills and into vineyards. Falcons in vineyard nests had higher nest attendance, higher brooding rates, and higher feeding rates than falcons in hill nests. Additionally, parents in vineyard nests fed their chicks a greater amount of total prey and larger prey items compared to parents in hill nests. I also found an absence of any significant diet differences between falcons in hill and vineyard habitats, suggesting that the latter may be a suitable alternative habitat for falcons. Because reintroduced juvenile falcons were released in areas devoid of adult falcons, it was possible that they were missing essential training normally provided by their parents. I used direct observations to demonstrate that the presence of siblings had similar effects to the presence of parents on the development of juvenile behaviour, with individuals flying, hunting, and playing more often when conspecifics were present. Finally, through the use of artificial nests and remote videography, I identified that falcons nesting in vineyards are likely to suffer lower

predation rates. I also found that falcons in vineyards are predated by a less dangerous suite of animals (such as hedgehogs, *Erinaceus europaeus*, and avian predators), than their counterparts in the hills, which are predated by more voracious species (such as stoats, *Mustela erminea*, and feral cats, *Felis catus*). The work presented in this thesis has also added to the current knowledge of New Zealand falcon breeding behaviour, prey preferences, and behavioural development.

Although agricultural regions globally are rarely associated with raptor conservation, and the ability of raptors to control the pests of agricultural crops has not been previously quantified, these results suggest that translocating New Zealand falcons into vineyards has potential for both the conservation of this species, and for providing biological control services to agriculture

ACKNOWLEDGMENTS

I could not imagine having completed this thesis without the support of my supervisors, and to both of them I am extremely grateful. Both Ximena Nelson and Jason Tylianakis have perfected the balance of giving a student the freedom to conduct independent research while also providing the perfect amount of support and guidance. I feel incredibly lucky to have been mentored by these two scientists, and am even more pleased that I can also call them both my friends. I'm incredibly thankful to Jason for putting up with hundreds of emails and phone calls about stats, for his ability to place this research within a wider context, and for always finding the time for a coffee with me despite his incredibly busy schedule. Only Jason would offer to have a meeting with me the day after a major earthquake in the midst of aftershocks and power outages.

My appreciation for Ximena's role in this thesis is beyond the written word. At our first meeting almost four years ago, I knew that she would be the best supervisor for me, but couldn't imagine just how far she'd go for her students. She's driven over farm tracks to meet me after an earthquake did away with her road, and gotten caught upside down in a fallen tree while searching for falcon nests with me. Ximena has managed to answer my emails with superhuman speed, has taught me how to apply for grants and give conference presentations, and has generally ushered me through the process of becoming a 'real scientist'.

There have been a heap of landowners who have not only given me access to their properties for my research, but have welcomed me into their homes for a cuppa, have shared their falcon stories with me, and have showed (or feigned) interest in what exactly my research was all about. I particularly thank Rowland and Jenny Mapp at Spray Point station for pointing me in the direction of my first falcon nest, the Watson family at Stirling Brook Station, the Stace family at Brookby farm, Fen Leov at Barracks farm, and the owners of Richmond Brook station. Denis Parsons and Garry Tait at Nelson Forests Ltd. assisted in getting me reports of dive-bombing falcons, and arranging access to their land. I also especially thank Ewan Rentoul and his sons Jason and Sam at Wye Hills farm for tolerating the foreign girl in her 'chick car' hooning around on their tracks, and Duncan Grigg for coming out and pulling my car out of the mud at 9 o'clock on the first evening he gave me access to his farm.

All of the vineyard owners and operators have also been incredibly welcoming. Richard Clare at the Ned/ Marisco has been a great friend since the start of my thesis, and I always look

forward to catching up with John Argyle and his staff at Brancott Estate. I'd also like to thank Peter Lamb at Cloudy Bay, Rod Brailsford and his staff (and smudge!) at Stoneleigh Estate, Adam McCone at Johnson Estate, Barry Feickert at Wainui Vineyard, Andrew Hammond at Lion's Back vineyard, Max Gifford at Stembridge vineyards, Aaron and Wayne at Yealands Estate, Owen Glover at Keresley vineyard, and the team at Winegrowers of ARA.

Dean Harliwich was good enough to give up a month of his summer holidays to help me radiotrack falcons. Elle Soper, on a summer scholarship, assisted with all manner of falcon related work and was by far the most tenacious fieldworker I've ever seen. Jack Knott and Brody Halkett also assisted with data collection for some parts of this work. Rosanne Homewood helped with video scoring and Kristy Udy helped with processing bird samples.

I'd like to thank Dr. Nick Fox for suggesting that the Falcons for Grapes would be a good project upon which to base a PhD. Colin Wynn, the FFG project manager, has also been helpful in putting me in touch with landowners and helping to facilitate the installation of cameras at vineyard nests. Lena Olley, who was an FFG volunteer for every summer of my fieldwork, kept me in the loop on what was happening with falcon work, accompanied me on multiple missions to search for falcon nests and was a great friend to me. I'd also like to thank Kate Morgan, Paul Lintott, Jamie Cooper, James Crowe, Ben Kay-Coles, Xavier Birch, Jeremy Kumagai, Richard Seaton, Terri Fisher, Jos Fryer, Tomas Kunca, Jack Ward and Mia Jesson for each helping me with fieldwork in one way or another. Additionally, the Raptor Association of New Zealand and Wingspan Birds of Prey Trust (especially Noel Hyde, Susie Curry, and Andrew Thomas) have provided me with advice and assistance.

The community of friends that I have made here in Blenheim have made it possible to work away from the University. Kathy and Eric Hughes have become like family to me, and not only coordinated purchasing radiotracking equipment and getting electrical work done for my camera systems, but also put me in touch with all the right people, and always knew when I needed a glass of wine and a shoulder to cry on. The trustees of the Marlborough Falcon Conservation Trust have become my greatest allies and have provided me with loads of support and words of encouragement. Andy Frost has given me advice and input throughout this thesis and was instrumental in feedback and editing for my talk for the Society for Conservation Biology conference. Mike Bell from OSNZ has taken me out bird banding and invited me in for a cup of tea with his family to talk all things bird related.

Peter Gaze at DoC has gone out of his way right from the start to help me weave my way through the sometimes contentious world of raptor research in New Zealand, to ensure I

had the appropriate permits for my work, and to use his network of connections to help put me in touch with the right people when I needed to be. Phil Bradfield has also always been there with an offer of advice and bit of cheeky humour. Paul Scofield at the Canterbury Museum provided me with a springboard from which to dive into the feather identification and helped with the ID of some of the trickier species. After the earthquakes, Gillian Stone, Alan Tennyson and Colin Miskelly helped me with finishing off my feather identifications.

Even though I spent most of my time in Marlborough over the course of this study, I've always felt welcome upon returning to the University. Thanks to Selwyn Cox and Nicole Lauren-Manuera, who have helped me wade through the paperwork. Jenny Ladley has been instrumental in helping me find lab space and equipment in a jiffy. Matt Walters, Alan Woods, Liz Fitzgerald, Nicky Judson and Penny Moore have all given me a hand over the years. Thanks also to Lucy Johnston in the postgraduate office. Jim Briskie has given me valuable advice and has helped with providing freezer space and specimens for my feather analysis and nutritional study. Andy Pratt has given me plenty of great guidance and can cook one hell of a Beef Bourguignon. My friends at University have been great! Thank you all for making me smile! Also, a big thanks to my flatmates in Christchurch over the years- Greer, Adrienne, Rob, Boss, Nat, Mels and Scott.

This research has been supported by a University of Canterbury Doctoral Scholarship. I have also had financial support for research costs from the Brian Mason Scientific and Technical Trust. Canon New Zealand gave me their Environmental Grant in 2008 with which I was able to obtain a fantastic pair of binoculars, cameras, and a video camera. Pernod Ricard New Zealand sponsored my work with the purchasing of radiotracking equipment and by providing me with electrical assistance. Craig (Monkey) Monk helped with the electrical work for the remote videography systems.

Thanks to my family for tolerating the fact that to do this research I've lived on the opposite side of the world from them- thank goodness for Skype! I am especially grateful for my wonderful parents for always encouraging me to pursue my goals. I am very lucky to come from such a fantastic family. Finally, thanks to my husband, Hayden Oliver, for putting up with me talking about nothing but falcons for four straight years, for coming out to search for falcon nests with me instead of going fishing, and for his unrelenting support and love.

PREFACE

Agriculture is considered to be the greatest extinction threat to birds (Green et al. 2005). Globally, 35% of the world's ice-free land surface is managed for primary production (Foley et al. 2007), but in countries like New Zealand, where agriculture is a dominant component of the economy, this figure can rise to 60% (MacLeod et al. 2008). Persistent expansion and intensification of the global agricultural landscape to feed a growing human population not only threatens the world's rare plants and animals (Foley et al. 2007), but threatens to reduce the ecosystem services (valued at US $33 trillion per year; Costanza et al. 1997) upon which humanity relies (Tilman et al. 2002).

Historically, the conservation of biodiversity has been focused on saving remnant areas of natural habitat by setting them aside for protection. More recently, attitudes around nature conservation have begun shifting away from this 'fire-brigade' approach (Edwards & Abivardi 1998), and toward the possibility that agroecosystems could be managed to be more wildlife friendly (Daily 2001; Fisher et al. 2011). It is possible that, simultaneously, agroecosystems could reap the benefits of increased functional diversity and ecosystem services on their land (Daily et al. 2000). Despite ample evidence to the contrary, there are indications that some species, including even the most specialised of species (e.g., Florida scrub jay, *Aphelocoma coerulescens*; Davison & Fitzpatrick 2010), can thrive within primary production systems.

The New Zealand falcon (*Falco novaeseelandiae*) is a nationally threatened species (Miskelly et al. 2008), and is the country's only remaining endemic bird of prey. This thesis focuses on the 'Eastern' form of the falcon, which is thought to occur East of the Southern Alps on the South Island of New Zealand (Fox 1977). Like all New Zealand species, falcons evolved without the presence of land-dwelling mammals, and therefore lack the morphological and behavioural adaptations necessary to deal with mammalian predators (Wilson 2004). These falcons often nest in 'scrapes' on the ground, and are therefore prone to high rates of nest predation by introduced mammals, and persecution is thought to occur (Fox 1977; Lawrence 2002). A 1970's survey predicted that between 3,000 and 4,500 pairs existed at the time (Fox 1977), and recent evidence indicates that falcon populations have since declined (Gaze & Hutzler 2004). To combat this decline, a project called 'Falcons for Grapes' (FFG) was started

in 2005 with the aim of re-establishing a population of falcons on the Wairau Plain in the Marlborough region of New Zealand's South Island. The programme sought to join the fields of agricultural pest management with predator conservation by releasing falcons into vineyards where it was thought they would provide a natural form of pest control.

Reintroductions are "an attempt to establish a species into an area which was part of its historical range, but from which it has been extirpated or become extinct" (IUCN 1998). This conservation method has become commonplace, especially in areas with high levels of threatened species such as New Zealand, however reintroductions are expensive, have low success rates, and are rarely reported on accurately or designed with scientific initiatives *a priori* (Griffith et al. 1989; Wolf et al. 1996; Fisher & Lindenmayer 2000; Armstrong & Seddon 2008).

Vineyards are particularly vulnerable to the destructive feeding patterns of passerine (perching) birds, as they represent an abundant and easily targeted food source in summer and autumn (Saxton et al. 2004). This presents a significant economic cost: in Marlborough alone this damage is estimated at over two million dollars per annum (Boyce et al. 1999). The innovation of the FFG scheme is that, by relocating falcon chicks to vineyards, it aimed to create self-sustaining conservation whereby an increase in falcon numbers, as new habitat and an abundance of prey were made available to them, would concomitantly create a form of integrated pest management for decreasing the detrimental effect of passerines in vineyards. Consequently, the FFG initiative had the potential to be strongly beneficial to both falcons and vineyard operators.

The 'vineyard' population of falcons is managed, but is also wild in sense that the birds are free to fly where they wish and return to the 'wild' population if they want. The presence of this well-monitored managed population, all sourced from the surrounding 'wild' population of falcons, provides a unique opportunity for studying the effects of reintroduction on the behaviour and survival rates of the falcons. Raptor conservation programmes generally reintroduce birds into habitats that they are known to naturally inhabit, whereas this scheme reintroduces falcons to vineyards, which is a habitat that they are not known to breed within naturally. It is therefore possible to determine if and how the vineyard-dominated landscape of the Wairau valley changes hunting and feeding behaviours, territory size, and population dynamics of the falcons.

Preface

The goals of predator conservation and agriculture are rarely parallel, and therefore very few predator conservation programmes have been centred in areas of intense agriculture. In our increasingly populated world, the interactions of raptors and agriculture will become increasingly important. This study presents an exceptional opportunity to examine the interrelationship between conservation and agriculture in a New Zealand setting. Significantly, the results of this research should prove useful for both the scientific and farming communities, as it will be the first study of this type to address whether this unique kind of conservation scheme can be successful, and thus will provide the platform from which future conservation and pest management alliances can be forged.

Although the success of the FFG scheme relies on knowledge of the effects it is having on the numbers, behaviour, and ecology of both falcons and passerine species within vineyards, prior to the onset of this PhD, no rigorous studies had taken place to determine this. Consequently, it is unclear whether the FFG scheme is successful at either of its two aims: conserving falcons, or reducing grape damage caused by pest bird species. Using a two-pronged approach, this thesis will address these important lacunae.

Chapters 2-7 are written as stand-alone scientific papers, the combination of which paint a picture of the efficacy of reintroducing falcons into vineyard habitat for pest control and falcon conservation. Each paper has been written so that it can be read independently, and in order to provide the necessary background information within each chapter, there inevitably is some repetition of material.

This study has been a collaborative effort, but the writing and analysis presented here are predominantly my own. Contributions of additional authors are listed in the acknowledgments within each chapter. All of the chapters presented here have been published or are currently submitted to scientific journals, and the reference for each paper is listed at the start of the corresponding chapter. Within the text of this thesis, all papers are referred to by their chapter number, including those that have already been published, for ease of reading. Figures and tables are numbered within each chapter, but references have been compiled at the end of the thesis to avoid repetition.

This research was conducted according to relevant national and international ethics guidelines and permits were provided by the University of Canterbury (2008/27R) and the New Zealand Department of Conservation (NM-23677-FAU).

CHAPTER ONE

INTRODUCTION

Adult female falcon kekking (a territorial call) near nest. (Photo: S. Kross)

BIOLOGICAL PEST CONTROL SERVICES BY BIRDS IN AGRICULTURE

Agricultural systems represent one of the largest terrestrial biomes on the planet (Foley et al. 2005), covering over 35% of the world's ice-free land (Foley et al. 2007). Humans appropriate over 23% of global net primary production, but in regions of intense agriculture this figure can be as high as 60 -100% (Haberl et al. 2007). Furthermore, growing human populations over the next few decades will result in greater pressure on the agricultural and natural landscapes of the globe (Tilman et al. 2002).

Agricultural intensification drives biodiversity loss (Sala et al. 2000; Geiger et al. 2010). Biodiversity is important for the functioning of healthy ecosystems at multiple scales, ranging from the individual field level to the entire biosphere, and human life relies on the ecosystem services that are provided by this functional biodiversity (Tilman et al. 2002; Diaz et al. 2006; Perrings et al. 2006). It is difficult to place a price tag on ecosystem services (Daily et al. 2000), but these have been valued at a minimum of US $33 trillion per year, and include global processes such as carbon sequestration, the water cycle, and air purification, as well as more localised processes such as pollination and biological pest control (Costanza et al. 1997).

Birds provide a number of ecosystem services at the provisioning, cultural, regulating, and supporting categories, as identified by the Millennium Ecosystem Assessment (2003). Examples of provisioning services include the production of fibre and food; cultural services include aesthetic value, spiritual enrichment, and recreation; and supporting services include nutrient cycling and production of biomass (Millennium Ecosystem Assessment 2003). This thesis will focus specifically on biological pest control, which is a regulating service, that along with pollination and seed dispersal, is considered to be one of the most important ecosystem services provided by birds (Şekercioğlu 2006).

In addition to Kirk et al.'s (1996) comprehensive review of avian control of insect pests in North American agriculture, there have been a number of recent broad reviews of avian ecosystem services (Şekercioğlu 2006; Whelan et al. 2008; Wenny et al. 2011). However, aside from Kirk et al. (1996), none of these reviews focus specifically on the role of birds for biological control in agricultural habitats, possibly because such studies are rare. For example, a meta-analysis of the top-down trophic cascades caused by birds included 29 original studies, only six of which were from agricultural systems (Mantyla et al. 2011). That comparatively few

studies have focused on quantifying the biological control services of birds in agriculture is surprising given the potential economic benefits associated with such services. Here, I review studies that have focused on the role of birds in controlling agricultural pests (Table 1.1).

Biological control

> "Nowhere are the consequences of biodiversity reduction more evident than in the realm of agricultural pest management"
>
> -Altieri 1999, p. 23

Biological control of pest organisms (hereafter: 'biological control') is defined as "the use of living organisms to suppress the population density or impact of a specific pest organism, making it less abundant or less damaging than it would otherwise be" (Eilenberg et al. 2001, p. 390). There are 4 types of biological control: classical biological control, inoculation biological control, inundation biological control, and conservation biological control. The first three types of control apply to the intentional and managed release of control organisms, often exotic species, into agricultural systems. The fourth, conservation biological control, is defined as "modification of the environment or existing practices to protect and enhance specific natural enemies or other organisms to reduce the effect of pests" (Eilenberg et al. 2001, p. 396). This thesis focuses on a reintroduction of threatened New Zealand falcons (*Falco novaeseelandiae*) into vineyards. This reintroduction does not fit cleanly into any one of the biological control categories, but can be considered a combination of conservation biological control and inundative biological control, where organisms are released over multiple occasions to maintain a population of natural enemies. One factor of all of the control methods listed above is some degree of targeted human management or manipulation. However, in many cases involving birds, the control services offered occur naturally, with no purposeful input by managers. Here, I refer to all cases where an animal controls a pest species as 'biological control', regardless of whether the biological control is part of a specific management regime. The study of ecosystem services provided by birds to farms is often dubbed 'economic ornithology' and was a prominent field in the study of biological control prior to the rise of pesticide use (Evenden 1995; Kirk et al. 1996).

The chemical advances made during the green revolution removed some of the need for natural biological control, but also led to an increasing reliance upon the use of chemicals to control pest species (Evenden 1995). Between 1961 and 1999 there was an 854% increase in the worldwide production of pesticides (Green et al. 2005). Even with this high reliance upon chemical control for pests, annual biological pest control services are estimated to be worth US $417 billion globally, including biological control services worth US $24 billion in cropland (Costanza et al. 1997). Concern has been expressed over the ramifications of the widespread use of chemicals and poisons for pest control, which can affect species well beyond the target organisms in fields (Geiger et al. 2010). These non-target species often include the predatory arthropods and birds (Bouvier et al. 2010) that would otherwise impart predation pressure on the target pest species. Pesticide use therefore reduces the power of biological control of pests and leads to further reliance upon chemical control. Establishing and protecting agroecosystems that take advantage of functional diversity to provide ecosystem services at the farm, landscape, and ecosystem levels, is seen as a way to simultaneously decrease chemical inputs and increase biodiversity (Daily et al. 2000; Perrings et al. 2006; Cumming & Spiesman 2006). To this end, there have been calls for biodiversity conservation to be expanded beyond the reserve system (Edwards & Abivardi 1998; MacLeod et al. 2008; Chazdon et al. 2009). Bringing together these two mindsets can potentially result in a win-win situation for both conservation and agriculture. Furthermore, demonstrating the role of large predators such as raptors in providing ecosystem services may aid in mitigation of the human-wildlife conflicts that often exist around these species (Gross 2008; Thirgood & Redpath 2008).

Birds for pest control

The use of conservation biological control has primarily focused on the management of habitats for the predatory arthropods that reduce the abundance of arthropod pests (e.g., Chiverton & Southerton 1991; Landis et al. 2000). Less research has focused on the use of vertebrates for biological control because they are more difficult to manage and do not respond to increasing arthropod pest numbers as quickly as invertebrate predators do.

Vertebrates and agriculture have a mixed history. Many vertebrates are considered pests, and virtually every food crop grown is threatened in some way by the foraging of birds,

which potentially causes billions of dollars in damage to crops each year (based on regional figures in De Grazio 1978, Ward 1979, and Bomford & Sinclair 2002). However, prior to the onset of the green revolution and the intensive use of pesticides on farms, many avian species were appreciated for their ability to control outbreaks of pest insects and even pest mammals (Forbush 1908; Whelan et al. 2008). In some extreme cases, the arrival of flocks of birds to forage upon pest outbreaks was seen as divine intervention, and historical accounts are filled with tales of birds rescuing gardens, fields, and even whole forests from exploding pest populations (Forbush 1908, Table 1.1).

Despite their role as pests themselves, birds can also have a beneficial impact as the natural enemies of agricultural pests in a number of production systems, ranging from coffee, to rice, vineyards, corn, and hops (Table 1.1 and references therein). In all of these cases, the birds are in some way benefitting from foraging within an agricultural matrix, while at the same time assisting the farmers themselves. This type of mutually beneficial relationship is not commonly quantified through scientific studies, but may increase the potential conservation value of farms. Importantly, there has been little conclusive research into the economic benefits of bird predation on farm pests.

The bulk of historical studies into the potential of birds for biological control have focused on describing gut contents or observations of the feeding behaviour of birds (Kirk et al. 1996). These studies, while useful in identifying the natural enemies of some pests, do not necessarily correlate with actual biocontrol services. The inability of early studies to prove actual economic services by birds contributed to the decline of economic ornithology following World War II (Kirk et al. 1996). However, these descriptive studies can reveal foraging trends that indicate ways in which birds provide biological control in agriculture. For example, agricultural land near coastal areas in the Pacific Northwest of North America is important non-breeding habitat for shorebirds, some species of which are likely to provide farmers with biological control services by consuming large numbers of invertebrate pests (Evans-Ogden et al. 2007).

The few studies that measure the effect of bird predation on pest abundance and/or damage to crops are generally exclusion studies or supplementation studies. Exclusion studies use nets or cages to prevent birds from accessing plants while still allowing access to invertebrates. Supplementation studies increase the abundance of birds either through direct

translocation of individuals into a treatment area, or through increasing the available habitat for birds through constructing perches or nest boxes, or planting crops to provide increased cover and/or alternate food sources. The latter technique is the most relevant for this thesis, as I have studied a system in which a predator has been purposefully reintroduced.

Trophic cascades

Successful biological control is reliant upon a trophic cascade existing between the control organism, the agricultural pest, and the agricultural product itself (Schmitz et al. 2000), whereby the control organism exerts predation pressure on the pest, which then damages less of the crop. For example, in temperate deciduous forests, insectivorous birds reduce the abundance of insects on trees, which causes a reduction in the leaf area lost to folivores, and creates a 30% increase in the above ground biomass of the trees (Marquis & Whelan 1994).

Predators, particularly apex predators at the top of this trophic cascade, can play an important role in maintaining ecosystem function (Estes 1996), and provide the bulk of biological control services (Dobson et al. 2006). Importantly, reductions in biodiversity due to human activities, such as reducing available habitat, are likely to first impact species from higher trophic levels (Holt et al. 1999), and can therefore impact biological control services without negatively affecting the pest species themselves (Dobson et al. 2006). This is highlighted in the vineyards of New Zealand, where the localised extirpation of the New Zealand falcon, the only remaining apex predator that primarily hunts for birds, has resulted in a system with extremely high densities of introduced pest species. In Chapter 2, I examine whether reintroducing falcons into vineyards has also re-established a trophic cascade through the reduction of pest bird abundance and damage to grape crops.

Intraguild predation and competition amongst predators

Trophic cascades can be affected by plant characteristics, such as chemical defences (Schmitz et al. 2000) and by intraguild predation and competition (Boege & Marquis 2006). In a review of 113 experiments, Mooney et al. (2010) found that predation by vertebrates reduces the abundance of predatory arthropods, potentially confounding, or even removing, the beneficial effect of arthropod predators. However, the authors also found that vertebrate predators

suppress the abundance of herbivores, reduce plant damage, and increase plant biomass (Mooney et al. 2010). Studies that have measured the impact of bird predation on arthropod predators have had mixed results, as have studies that have ranked the importance of bird versus arthropod predation on pest species abundance. In one example, hop plants (*Humulus lupulus*) that were covered by bird exclusion netting had higher abundance of hop looper pest (*Hypena humuli*). Hop loopers inside exclusion nets had higher rates of parasitism, compared to those on plants in non-exclusion or total insect exclusion treatments, suggesting that bird predation was acting upon both the hop looper and its parasitoids (Grasswitz & James 2011). However, a replicate of the same treatment groups the following year showed no difference between parasitism rates in bird-exclusion and open treatments (Grasswitz & James 2011). Most other studies that compare predation by birds and predation or parasitism by invertebrates have obtained results suggesting that the two guilds exert additive effects upon pest populations. Birds tend to actively forage upon larger insect prey (> 5 mm) while invertebrate predators tend to forage upon smaller insects (Hooks et al. 2003; Borkhataria et al. 2006; Remmel et al. 2011), suggesting that these predators target different prey groups and therefore compliment each other.

Examples of the importance of bird predation on pests as compared to arthropod predation on pests have been reported in a number of different crop systems. A review by Remmel et al. (2011) showed that while folivorous insect larvae on trees were predated more by arthropod predators than by bird predators, the predation rates by birds were less variable. In a shade-grown coffee plantation, birds and lizards had an additive effect on pest abundance, and the presence of these vertebrate predators did not decrease the incidence of parasitism by wasps (Borkhataria et al. 2006). In a *Brassica* farming system, birds were deemed to be more important predators of folivores than were invertebrates (Hooks et al. 2003). Similarly, in chickpea crops, birds and parasitoids were shown to have additive effects on gram pod borer (*Helicoverpa armigera*) and to increase yield by 44% (Gopali et al. 2009). Finally, in Africa, models of the importance of arthropod and bird predators in influencing Senegalese grasshopper (*O. senegalensis*) abundance and egg-hatching rates showed that while intraguild competition did occur, the combined impact of both guilds was higher than the impact of either individual group (Axelsen et al. 2009). While none of these examples apply to non-arthropod pest species, they do illustrate that maintaining a suite of natural enemies from multiple orders provides a

wider range of beneficial species and therefore provides insurance and complementarity to biological control.

Habitat complexity

In order to maintain a more diverse assemblage of natural enemies, agroecosystems must be maintained with high levels of habitat heterogeneity. Agricultural intensification results in the simplification of habitat complexity at the field and landscape levels (Tscharntke et al. 2005). For invertebrates, functional complementarity and niche overlap is linked to the effect size and stability of biological control services (Landis et al. 2000; Snyder et al. 2006; Tylianakis et al. 2006). However, the diversity of natural enemies within an agricultural system is largely dictated by the complexity and diversity of habitat types available within that landscape (Tscharntke et al. 2007). With decreasing habitat complexity, the absence of refugia, suitable perches, or alternate food sources can become the limiting factors in the biological control of pests (Thies et al. 2011). For birds, landscape features such as hedgerows have been linked with increased biological control (Marshall & Moonen 2002), as has the planting of refuge- and alternate food- crops (Jones & Sieving 2006; Gopali et al. 2009).

The effects of bird predation on insect pests has been studied most extensively in coffee agroecosystems. Shade-grown coffee farms with more diverse structure and plant species richness harbour a greater diversity and abundance of avian species (Greenburg et al. 2000), and this can have an impact on the biological control services applied by birds (Perfecto et al. 2004; Kellermann et al. 2008; Van Bael et al. 2008; Philpott et al. 2009; Railsback & Johnson 2011). The black-throated blue warbler (*Dendoica caerulescens*), the most significant predator of coffee berry borer in Jamaican coffee farms (Kellermann et al. 2008), prefers to roost overnight in large trees and continuous forest, suggesting that simplification of the agricultural matrix would result in reduced biological control services from this species (Jirinec et al. 2011).

In a chickpea (*Cicer arietinum*) agroecosystem in India, constructing artificial perches and planting 'live perch' crops such as sunflower and sorghum reduced the abundance of the pest *Helicoverpa armigera* (Gopali et al. 2009). Constructing artificial perches alone, which would only increase the abundance of birds and not affect the abundance of invertebrate natural enemies, resulted in a 40% reduction in larvae of *H. armigera* and a 44% increase in yield (Gopali et al. 2009). Additionally, the planting of live perches not only increased bird predation,

but also increased parasitoid abundance and acted as a trap crop for the pest larvae. The combination of these conservation biological control outcomes decreased pest abundance and increased chickpea yield at a similar rate- but significantly lower cost- than pesticide treatment, and therefore had a higher net gain than pesticide treated crops (Gopali et al. 2009).

Numerical and functional responses

> "The position occupied by birds among the forces of nature is unique in one respect at least; their structure fits them to perform the office of a swiftly moving force of police, large bodies of which can be assembled at once to correct disturbances caused by abnormal outbreaks of plant or animal life. This function is well performed. A swarm of locusts appears, and birds of many species congregate to feed upon locusts. An irruption of field mice, lemmings, or gophers occurs, and birds of prey gather to the feast from far and near."
>
> -Forbush 1908, p. 2

Birds are capable of responding both numerically and functionally to outbreaks of insect pests (Whelan et al. 2008), as is the case for the natural avian predators of the pine processionary moth (*Thaumetopoea pityocampa*; Barbaro & Battisti 2011), a folivorous species that costs European pine plantations millions to control annually (Cayuela et al. 2011). Because of their high mobility and ability to detect fluctuations in prey densities, birds can respond to outbreaks of prey populations quickly and sometimes in high numbers (e.g., raptors and fluctuating vole populations; Korpimäki & Norrdahl 1991). A study of great tit (*Parus major*) predation on experimentally-placed codling moth (*Cydia pomonella*) larvae in apple orchards showed that at higher larvae densities, individual birds increased their search effort, and subsequently removed a greater percentage of the larvae (Solomon & Glen 1979). Birds can also provide ongoing suppression of pests, even at low pest numbers, with the potential to reduce the need for insecticide sprays. Encouragingly, Marquis & Whelan (1994) found that the effect of insectivorous birds alone halved the damage caused by herbivorous insects to foliage, with the additive effect of insecticide spraying reducing damage by half again.

Top predators such as raptors and carnivorous mammals are also capable of a density-dependent response to increasing prey populations, but only up to a certain threshold (Sinclair et al. 1990). Because top predators are generally territorial, and have slow reproduction rates compared to lower-order predators such as insectivores, their response to increasing prey

populations is limited by the number of individuals that can hunt in an area, as well as by the amount each individual can consume (Sinclair et al. 1990).

Table 1.1. The role of birds in controlling agricultural pests. Beneficial species, if specified in individual studies, are listed, as are the type of study, the measured change in pest populations as a result of avian foraging, and the change in damage as a result of avian foraging (if measured). *Supplementation* studies used methods to increase the number of birds in an area through provisioning of nesting or perching habitat, or by purposefully reintroducing a species into an area. *Exclusion* studies used nets or cages to prevent birds from foraging within a certain area of the crop. *No treatment* studies relied on observations of birds foraging on pest species or examination of bird gut contents to make assumptions about the role of birds in reducing pest numbers. Most *No treatment* studies are historical accounts.

Table 1.1. The role of birds in controlling agricultural pests

Agricultural system	**Beneficial Species**	**Study type**	**Change in pest populations**	**Change in damage**	**References**
Vineyards	New Zealand falcon (*Falco novaeseelandiae*)	Supplementation (reintroduction)	Reduced abundance of introduced European pest birds by 78-83%, did not reduce the abundance of the native silvereye (*Zosterops lateralis*)	Reduced incidence of grape removal (-95%) and grape pecking (-55%) when falcons present. Overall savings to growers estimated at US $234-326/ha depending on grape varietal	Kross et al. 2011 (Chapter 2)
	Western bluebirds (*Sialia mexicana*) and insectivorous species	Supplementation (nest boxes)	Reduced the number of experimentally positioned live beet army worms (*Spodoptera exigua*) by 59%, with highest removal rates observed closest to supplemented nest boxes	Not measured. Experimentally positioned insects were a model for other potential pest species.	Jedlika et al. 2011
Hops	Insectivorous birds	Exclusion	Predated upon and reduced hop looper (*Hypena humuli*) larvae, although reductions were not statistically significant and invertebrate predators were more important	Not measured	Grasswitz & James 2011
Corn/ Maize	Omnivorous and Insectivorous birds	Exclusion	Reduced densities of cutworms (*Agrotis* spp) and weevils (*Sphenophorus* spp.), European corn borer (*Ostrinia nubilalis*), corn leaf aphids (*Rhopalosiphum maidis*) significantly	Reduced damage by weevils when birds were allowed access and closer to bird shelter. No change in crop yield, but infestation levels of all pests were low during study	Tremblay et al. 2001
	American crow (*Corvus brachyrhynchos*)	Exclusion	Reduced over-wintering larvae of European corn borer by 50%	Not measured	Quiring & Timmins 1988 (in: Kirk et al. 1996)
Brassicas	Insectivorous birds	Exclusion	Reduced densities of two damaging lepidopteran caterpillars (*Artogeia rapae* and *Trichoplusia ni*)	Reduced folivory by caterpillars and increased plant productivity	Hooks et al. 2003

Table 1.1. The role of birds in controlling agricultural pests

Agricultural system	**Beneficial Species**	**Study type**	**Change in pest populations**	**Change in damage**	**References**
Tea	Asian-pied starling (*Sturnus contra)*, jungle myna (*Acridotheres fuscus)*, chestnut-tailed starling (*Sturnus malabaricus)* red-vented bulbul (*Pycnonotus cafer)*	No treatment-Behavioural study	Predated large numbers of caterpillars that defoliate crops, including the invasive *Hyposidra talaca*	Not measured	Sinu 2011
Cocoa agroforestry	General insectivores (27 species)	Exclusion	Reduced abundance of large and small arthropods	Reduced leaf damage	Van Bael et al. 2007
Citrus	General insectivores and omnivores	Exclusion	Exclusion of birds resulted in increases of dermaptera which are sometimes pests in other crops (but are also known to eat pests such as aphids). Exclusion of birds did not decrease other arthropods	Not measured	Piñol et al. 2010
Coffee	General insectivores	Exclusion	Reduced abundance of arthropods on coffee plants	Not measured	Philpott et al. 2009
		Exclusion	Reduction in large arthropods (>5mm) by 64-80%	Reduction in leaf damage	Greenberg et al. 2000
		Exclusion	Reduction in arthropod abundance. Reduction was larger in shade-grown systems, but incidence of fungal infection was higher	28% Reduction in leaf damage	Johnson et al. 2009
		Exclusion	4x reduction in the abundance of flatid planthopper (*Petrusea epilepsis*) but had no effect on abundance of coffee leafminer (*Leucoptera coffeella*)	Not measured	Borkhataria et al. 2006

Table 1.1. The role of birds in controlling agricultural pests

Agricultural system	**Beneficial Species**	**Study type**	**Change in pest populations**	**Change in damage**	**References**
Coffee	General insectivores	Exclusion	14% significant reduction in the incidence of coffee-berry borer (*Hypothenemus hampei*) infections	Infected berries cannot be sold so infection rates= damage rates. Economic analysis showed a savings of US $44- $105/ha	Kellermann et al. 2008
		Exclusion	Suppressed simulated outbreaks of lepidopteran caterpillars, with a greater effect of bird presence on predation of caterpillars in more complex shade-grown coffee	Not measured	Perfecto et al. 2004
Sugar Maple	Insectivorous passerines	No treatment	Predated upon forest tent caterpillars (*Malacosoma disstria*) that were causing significant damage in 1897-1898 and reduced the abundance of these insects by 1900 so that damage was no longer noticed	Not measured	Forbush 1908
Apples	Great tit (*Parus major*)	Exclusion & supplementation (nest boxes)	Increased length of time that birds could access trees led to reduced abundance of caterpillars	Reduced damage from 13.8% to 11.2%, increased yield of fruit from 4.7 to 7.8 kg/tree	Mols & Visser 2002
		Supplementation (nest boxes)	Not measured	Reduced caterpillar damage by 50% near nest boxes	Mols & Visser 2007
		No treatment-Experimental increase of moth larvae	Reduced the abundance of codling moth larvae in a density dependent manner. Between 47% and 100% of larvae were removed by bird predators	Not measured	Solomon & Glen 1979
	Blue tit (*Parus caeruleus*), great tit	Exclusion, experimental increase of moth larvae	Reduced the abundance of codling moth by 94-95%	Not measured	Solomon et al. 1976
	Silvereye (*Zosterops lateralis*)	Exclusion, experimental increase of moth larvae	Reduced the abundance of codling moth larvae in a density dependent manner	Not measured	Wearing & McCarthy 1992

Table 1.1. The role of birds in controlling agricultural pests

Agricultural system	**Beneficial Species**	**Study type**	**Change in pest populations**	**Change in damage**	**References**
Pears	Insectivores and omnivores	No treatment-behavioural study	Predation on large numbers of psyllas in winter	Not measured	Odell 1927
Pigeon pea	Jungle babbler (*Turdoides striatus*)	No treatment-Behavioural study	Control old-world bollworm (*Helicoverpa armigera*) in pigeon pea crops	Not measured	Bharucha & Padate 2010
Chickpea	General insectivores	Supplementation (perches)	Artificial perches alone (increasing bird abundance only) resulted in a 40% reduction in gram pod borer (*Helicoverpa armigera*). Artificial perches and live perches (sunflower and sorghum) increased effectiveness by also increasing abundance of invertebrate natural enemies and acting as a trap crop	Artificial perches resulted in a 44% increase in crop yield	Gopali et al. 2009
Millet	Range of insectivores and omnivores	No treatment	Models estimated the role of birds and invertebrate egg predators on the reduction of the Senegalese grasshopper (*O. senegalensis*). Simulated estimates were that birds alone accounted for between a 20% and 26% reduction in grasshoppers in millet. Bird predation pressure was estimated to reduce the following season's egg input by 34%	Not measured	Axelsen et al. 2009
Grain	Franklin's Gull (*Leucophaeus pipixcan*)	No treatment-behavioural observation	Flocked to a severe outbreak of Mormon crickets (*Anabrus purpurascens*) in Utah and controlled the numbers to save some crops. Perceived as "a heaven-sent miracle"	Not measured	Forbush 1908

Table 1.1. The role of birds in controlling agricultural pests

Agricultural system	**Beneficial Species**	**Study type**	**Change in pest populations**	**Change in damage**	**References**
Rice	Ducks	Supplementation (introducing domestic ducks)	'Pasturing' domestic ducks in rice fields at times when they will not harm the rice crop has been shown to have an 89% success rate for removing the highly invasive golden apple snail (*Pomacea canaliculata*) in some Asian countries	Not measured	Naylor 1996
Rice	All birds- noted were blackbird, plover, curlew, quail, prairie chicken (species not specified)	No treatment- behavioural observation	1865- locust outbreaks in the Mississippi valley. Different groups of birds were able to control pest numbers of some outbreaks. The United States Entomological Commission declared that the efficacy of birds for controlling pests "… so full and complete that it was impossible to entertain any doubt on this point."	Not measured	Forbush 1908
	Barn Owls (*Tyto alba*)	No treatment	Diet of owls was dominated by rodent pest species, especially when pest abundance was high, showing potential for biological control	Not measured	Granjon & Traoré 2007
Wheat	Ibis (*Threskiornis molucca*), spoonbills (*Platalea regia*), cranes (*Grus* spp.)	No treatment	In 1892 in Australia, swarms of locusts were descended upon by these birds and an outbreak was stopped	Not measured	Forbush 1908
Pasture	Goldfinch (*Carduelis carduelis*)	Exclusion & behavioural observations/ seed collection	32.2 % of seeds of the invasive nodding thistle (*Carduus nutans* L.) in pastures were husked by goldfinches	Only 19% of artificially sown seeds outside of exclusion cages survived, with only 15.6% germinating, however mice may also have predated seeds outside of cages	Kelly & McCallum 1990
Oil palm	General birds	Exclusion	Not measured	Reduced herbivory on youg plants by 66%	Koh 2008

Table 1.1. The role of birds in controlling agricultural pests

Agricultural system	**Beneficial Species**	**Study type**	**Change in pest populations**	**Change in damage**	**References**
Oil palm	Barn owls	Mixed	Mixed results in a number of studies reviewed, with a need for more research. Most studies did not attempt to monitor rat populations	Some studies found evidence of reduced fresh damage	Wood & Fee 2003 and references therein
Soybean	Diurnal raptors & barn owls	Supplementation (artificial perches)	Significantly fewer mice in fields with artificial perches compared to fields without perches. A higher density of perches was associated with fewer mice	Not detected. Mice numbers too low in either treatment for detectable damage	Kay et al. 1994

BIRDS OF PREY AND AGRICULTURE

> "The result proves that a class of birds commonly looked upon as enemies to the farmer, and indiscriminately destroyed whenever occasion offers, really rank among his best friends, and with few exceptions should be preserved, and encouraged to take up their abode in the neighborhood of his home."
>
> - C. Hart Merriam, chief of division & Hon. J.M. Rusk, Secretary of Agriculture, USDA 1893

As the natural enemies of most vertebrate pest species, raptors can provide unique biological control in a number of different agricultural systems. However, the role of raptors for biological control has rarely been quantified. In fact, prior to our publication of the results presented in Chapter 2 (Kross et al. 2011, see Appendix 3), there had been no formal assessment of the top-down effect of a raptor on a tri-trophic cascade in an agricultural setting. While raptors can provide economically beneficial biological control services, many species have suffered declines (Butchart et al. 2004), largely as a result of activities linked with agriculture, such as land clearing and the use of poisons for pest control (Ratcliff 1967; Table 1.2). Similarly, while agricultural regions can provide birds of prey with increased prey availability, they can also be filled with hazards that result in population declines, such as dangerous electro-utility structures and persecution by humans (Real et al. 2001; Marchesi et al. 2002; Lehman et al. 2007; Thirgood & Redpath 2008; López-López et al. 2011; Table 1.2).

Trained raptors have been used for biological control in a number of systems (Baxter & Allan 2006). In fact, a simple Google search for 'falconry pest control' resulted in over 30 different websites offering commercial pest control services through the use of falconry in the United Kingdom alone. Despite a number of professionals offering this service, the effects of falconry techniques for biological control has rarely been quantified. The few studies that have examined the efficacy of falconry techniques for pest deterrence have found that falconry can be effective, but that the effects are limited due to a need for intensive management, high costs, and a limited timeframe for effectiveness around the deployment of the falcon (Erickson et al. 1990; Soldatini et al. 2008). Kenward (1978) found that falconry was no more effective at dispelling wood pigeons (*Columba palmbus*) from brassica crops than the disturbances caused by nearby pedestrians, cyclists and horsemen.

For raptors to act as a form of natural biological control in agricultural landscapes, they must first be able to survive in such landscapes. Habitat loss is one of the most frequently cited causes of raptor declines globally, and expansion of agriculture is the most common cause of habitat loss (Foley et al. 2007). Although agricultural fields can be high in prey availability, in many cases, raptor use of these fields for foraging can be limited by a lack of suitable perches or nesting sites (Preston 1990; Widen 1994; Sheffield et al. 2001). This lack of perches combined with a high density of power lines in agricultural landscapes, can result in raptors perching on dangerous electro-utility structures and being electrocuted (Real et al. 2001; Lehman et al. 2007).

Birds of prey with more abundant food sources early in the breeding season lay larger clutches (Newton & Marquis 1981) and produce more fledglings (Wiehn & Korpomäki 1997; Palmer et al. 2001), resulting in greater breeding output. Agricultural fields and landscapes maintain unnaturally high densities of herbivorous and frugivorous rodents and birds, and for raptor species that can tolerate the human-modified landscape, these prey densities can result in increasing populations. Irrigated agricultural fields can also help to buffer against fluctuations in prey populations by providing a constant source of food even during dry conditions (Marti 2010). However, the large-scale changes that occur in agricultural fields with the onset of harvest can sometimes have negative effects on the breeding success of raptors that rely on the prey species available within a given crop (Martin et al. 2010).

Raptor species with the behavioural flexibility that allows them to breed and hunt in agricultural areas are less likely to have suffered the population declines seen in species intolerant of human-modified landscapes (Table 1.2 and references within). A review of the abundance of raptors in the metropolitan region in Chile showed that species able to tolerate agricultural or urban habitats were common, whereas those that specialised upon native vegetation were rare (Jaksic et al. 2001). In some cases, even where human activities and agricultural expansion have led to decreases in natural prey populations, opportunistic species or those with behavioural plasticity may be able to swap and forage upon exotic species. This is the case in New Zealand's vineyards, where a paucity of native bird species and abundance of exotic birds has led to falcons relying primarily upon introduced birds for prey (Chapter 4). Similarly, Andean condors (*Vultur gryphus*) in Patagonia have switched from a diet once

dominated by native species to one currently dominated by exotic livestock and game species, reflecting the changing landscape of the area (Lambertucci et al. 2009).

Land use changes due to agriculture can alter the makeup of regional raptor populations. For example, in the western regions of North America, the Swainson's hawk (*Buteo swainsoni*) has benefitted from an increase in agricultural fields and dense croplands (Schmutz 1987; Swolgaard et al. 2008), whereas in the same area, the ferruginous hawk (*Buteo regalis*) has declined because of a preference for the expansive grasslands that once occurred there and an intolerance to human activity near their nests (Schmutz 1987). In the Mongolian steppes, changes in land use have not affected the Eurasian kestrel (*Falco tinnunculus*) and lesser kestrel (*F. naumanni*), while species that specialise on steppe habitat such as the steppe eagle (*Aquila nipalensis*) and saker falcon (*F. cherrug*) have declined (Sánchez-Zapata et al. 2003).

For many birds of prey, agricultural expansion is a mixed blessing. Increases in food densities can be paired with an increase in mortality from anthropogenic sources such as poisoning, electrocution, and persecution. For example, the Eurasian eagle owl (*Bubo bubo*) in the Italian Alps benefits from high rodent densities in valleys dominated by agriculture, but their population is limited due to high rates of electrocution in the same areas (Marchesi et al. 2002). Similarly, in Spain, agricultural conversion has led to ponds on farms acting as surrogates for previously-drained wetlands and providing nesting and hunting locations for the marsh harrier (*Circus aeruginosus*). However, harriers in this region area are also prone to high electrocution rates (Cardador et al. 2011). The Mackinder's eagle owl (*Bubo capensis mackinderi*) in Kenya appears also to benefit from agriculture, due to an increased abundance and richness of prey species available on agricultural land compared with nearby grassland, although it suffers from high mortality due to primary and secondary poisoning by pesticides (Ogada & Kibuthu 2009).

While raptors can sometimes be beneficial to agriculture, such as through the provisioning of biological control services (see Table 1.1), many farmers continue to perceive raptors as a threat. The decline of birds of prey in many parts of the world has been augmented by incorrect assumptions surrounding raptors that led to popularised persecution, including government-backed bounty schemes (Barrow 2002). The expansion of human range across the globe has often been accompanied by declines in the number of large apex predators as a result of increased persecution in regions densely inhabited by humans (Woodroffe 2000). Persecution

arises as a result of raptor predation on domestic prey or game species, and often occurs when habitat change has caused a shortage of wild prey populations (Palma et al. 2006; Thirgood & Redpath 2008). Nevertheless, some raptor species actually benefit from urban landscapes because they are relatively free from persecution compared to the agricultural landscapes where people keep poultry and livestock (Chace & Walsh 2006). Most persecution of raptors targets breeding adults, with negative implications for population growth (Real et al. 2001; Whitfield et al. 2004; Virani & Harper 2009). This human-wildlife conflict is a longstanding custom in many agricultural and game-hunting areas, and can pose a major threat to the conservation of some threatened or recovering species (Newton 1979; Real et al. 2001; Whitfield et al. 2004; Thirgood & Redpath 2008). However, renewed interest in the role of raptors for providing ecosystem services in agriculture has seen farmers providing wild populations of raptors with perches or nest boxes in order to increase populations, and has also seen as an increase in studies on the ramifications of re-establishing raptor populations for biological control of pests (Kay et al. 1994; Meyrom et al. 2009; this study).

Table 1.2. The impact of intensive agriculture on different raptor species. The agricultural system (and what it is being compared to) is listed, as are the negative (-) and positive (+) impacts that were detected as a result of agriculture, and the studies from which this is based. (=) represents studies where no change was detected.

Table 1.2. The impact of intensive agriculture on different raptor species

Species	**Location**	**Agricultural System**	**Impact**	**References**
Lesser Kestrel *Falco naumanni*	Spain	Intensive modern agriculture (traditional agro-grazing)	(-) Smaller prey (-) Larger home-ranges (-) Lower productivity	Tella et al. 1998
	Mongolia	Cereals and irrigated crops (grasslands, saline steppe, and dry steppe)	(+) Abundance	Sánchez-Zapata et al. 2003
New Zealand falcon *Falco novaeseelandiae*	New Zealand	Intensive viticulture (low intensity grazing/ natural habitat)	(+) Prey abundance (=) Diet	Chapter 4
			(+) Increased nest attendance (+) Increased biomass fed to chicks	Chapter 5
			(-) Electrocution	Fox & Wynn 2010
		Pinus radiata forestry (no comparison)	(+) High breeding densities (+) High prey availability (+) Control of predators	Seaton et al. 2009

Table 1.2. The impact of intensive agriculture on different raptor species

Species	**Location**	**Agricultural System**	**Impact**	**References**
Mauritius kestrel (*Falco punctatus*)	Mauritius	Sugar cane agriculture (Native forest and grassland)	(-) Habitat (-) Lack of perches for hunting	Burgess et al. 2009
Eurasian kestrel (*Falco tinnunculus*)	France	Gradient of land-use intensity from woodlots and grassland areas to intensive arable agriculture	(-) Reduction of hedgerows, woodlots, and grasses used for foraging and shelter (-) Reduced prey availability	Butet et al. 2010
	Mongolia	Cereals and irrigated crops (grasslands, saline steppe, and dry steppe)	(+) Abundance	Sánchez-Zapata et al. 2003
Saker falcon (*Falco cherrug*)	Mongolia	Cereals and irrigated crops (grasslands, saline steppe, and dry steppe)	(-) Range (not observed in agriculture) (-) Prey abundance	Sánchez-Zapata et al. 2003
Northern Goshawk (*Accipiter gentilis*)	Norway	Nests in small forest patches in farmland (nests in extensive forest)	(-) Prey delivery rates (-) Diet diversity (=) Weight class of prey	Johansen et al. 2007
Snail kite (*Rosthramus sociabilis*)	Florida	Wetlands fragmented by agriculture and urbanisation (continuous wetlands)	(-) Reduced individual range (-) Less prey during drought conditions	Martin et al. 2006
Bonelli's eagle (*Aquila fasciatus*)	Spain	Study of the causes of mortality in multiple landscapes including flat agricultural land	(-) Electrocution	Real et al. 2001
Steppe eagle (*Aquila nipalensis*)	Mongolia	Cereals and irrigated crops (grasslands, saline steppe, and dry steppe)	(-) Range (-) Prey abundance	Sánchez-Zapata et al. 2003
Short-toed eagle (*Circaetus gallicus*)	Mongolia	Cereals and irrigated crops (grasslands, saline steppe, and dry steppe)	(-) Range (not observed in agriculture) (-) Prey abundance	Sánchez-Zapata et al. 2003
Montagu's harrier (*Circus pygargus*)	Mongolia	Cereals and irrigated crops (grasslands, saline steppe, and dry steppe)	(+) Breeding sites	Sánchez-Zapata et al. 2003
Pallid harrier (*Circus macrourus*)	Mongolia	Cereals and irrigated crops (grasslands, saline steppe, and dry steppe)	(-) Range (not observed in agriculture)	Sánchez-Zapata et al. 2003
Western marsh-harrier (*Circus aeruginosus*)	Spain	Modern, intensive agriculture (traditional non-intensive agriculture)	(+) Breed near ponds (+) Increased food availability (+) Expanding range	Cardador & Mañosa 2011; Cardador et al. 2011
Barn owl (*Tyto alba*)	Utah	Agricultural fields of hay, and barley (no comparison)	(+) Food availability (+) Less variation in prey abundance	Marti 2010
	Ohio	Agricultural fields of corn and	(-) Population declines due to	Colvin 1985

Table 1.2. The impact of intensive agriculture on different raptor species

Species	**Location**	**Agricultural System**	**Impact**	**References**
		soybean (grass-based agriculture)	change from hay production to corn and soybean	
Barn owl (*Tyto alba*)	Switzerland	Cereal grain fields (ecological compensation areas planted in wildflowers)	(+) Preferred to hunt in cereal fields despite high mammal abundance in wildflower areas, probably because of prey availability	Arlettaz et al. 2010
Eagle owl (*Bubo bubo*)	Italy (Alps)	Cultivated-urbanized valley floors (mountain slopes covered by woodland)	(+) Food availability (+) Higher productivity (+) Population density (-) Electrocution	Marchesi et al. 2002
Mackinder's eagle owl (*Bubo capensis mackinderi*)	Kenya	Irrigated farms (grazed, brushy grassland)	(+) Prey abundance (+) Prey richness (+) Diet breadth (-) Primary and secondary poisoning with pesticides	Ogada & Kibuthu 2009
Burrowing owl (*Athene aunicularia*)	Washington, USA	Agriultural landscapes vs. urban landscapes	(+) Nesting success (+) Prey availability (+) Fewer predators (badgers controlled by farmers)	Conway et al. 2006
Hawaiian hawk (*Buteo solitarius*)	Hawaii	Agriculture such as expansive sugar cane (native forest)	(-) Reduction in nest tree availability (-) Reduced range	Griffin et al. 1998
Augur buzzard (*Buteo augur*)	Kenya	Horticulture (acacia woodland-pasture & national forest)	(=) Intermediate breeding success in horticulture (-) High adult mortality from persecution	Virani & Harper 2009
Common buzzard (*Buteo buteo*)	France	Gradient of land-use intensity from woodlots and grassland areas to intensive arable agriculture	(-) Reduction of hedgerows, woodlots, and grasses areas used for foraging and shelter (-) Reduced prey availability	Butet et al. 2010
Ferruginous hawk (*Buteo regalis*)	Alberta, Canada	Agricultural fields of tall and dense crops (grassland)	(-) Density of hawks (-) Less tolerant of humans near nests	Schmutz 1987
Swainson's hawk (*Buteo swainsoni*)	Alberta, Canada	Agricultural fields of tall and dense crops (grassland)	(+) Hawk abundance (+) Higher reproduction rates	Schmutz 1987
	California	Vineyards, agricultural fields, urban areas (native habitat)	(-) Reduced foraging in vineyards (+) Increased foraging in irrigated hay and dry-land grain (although preference for shorter, recently mowed grasses)	Swolgaard et al. 2008
Andean condor (*Vultur gryphus*)	Patagonia, Argentina	Extensive livestock grazing (natural steppe and subantarctic forest)	(-) Reduction in natural prey (+) Increase in exotic prey such as livestock and game species (-) Poisoning through livestock treated with veterinary medicine, consuming poisoned	Lambertucci et al. 2009

Table 1.2. The impact of intensive agriculture on different raptor species

Species	**Location**	**Agricultural System**	**Impact**	**References**
			animals or animals shot with lead shot	

AGRICULTURE AND THE CONSERVATION OF PREDATORS

> "A conservation lesson to be learned from New Zealand is that protection alone is not enough"
>
> - Clout, 2001. p. 415

Avian populations are threatened by ongoing habitat modification for agriculture, as production landscapes infringe upon areas of natural habitat and existing agricultural regions intensify their production practices (Green et al. 2005; Foley et al. 2005). Conservation initiatives for threatened species rarely focus on areas of production, and instead hinge upon regions of remaining native vegetation, despite the ongoing loss of unaltered landscapes. Recently, calls have been made to extend conservation initiatives into agricultural regions, especially in areas dominated by agriculture such as New Zealand (Edwards & Abivardi 1998; MacLeod et al. 2008; Fischer et al. 2011). While reserves tend to be found in rugged and inaccessible areas of low economic value (Margules & Pressey 2000), production lands tend to be accessible and to have a high availability of resources, both natural and supplemented. Encouraging wildlife to return to production landscapes may benefit threatened species by opening up new habitat to them, and can simultaneously improve the functional diversity that provides ecosystem services such as pest control, pollination, and seed dispersal (Foley et al. 2005).

In areas where naïve prey reside, such as on oceanic islands, the introduction of exotic predators can result in population reductions and even extinctions (Blackburn et al. 2004). Feral cats (*Felis catus*), and invasive rats (*Rattus* spp.) have been spread widely across the world's oceanic islands and have been implicated in the decline or extinction of over 170 vertebrate species worldwide (Towns et al. 2006; Medina et al. 2011). Nowhere is the detrimental impact of these introduced species more apparent than in New Zealand, where exotic mammals have played a role in the decline of most of the 58 avian species that have become extinct since the arrival of humans, approximately 2000 years ago, and continue to threaten the existence of most remaining endemic species today (Wilson, 2004).

Reintroduction biology has been honed in New Zealand through the successful rescues of critically endangered species such as the Chatham Island black robin (*Petroica traversi*), the takahe (*Porphyrio mantelli*), and the kakapo (*Stringops habroptilus;* Wilson 2004). In these cases, individuals from small, threatened, populations were moved onto predator-free islands where they have been able to recover. Many threatened species remaining on the main islands of New Zealand are currently restricted to marginal habitat (Wilson 2004), and shrinking ranges and continued population declines are likely to prevent these populations from naturally re-colonising the productive low-lying regions in which most agriculture occurs. In the agriculture-dominated nation of New Zealand, agricultural landscapes could represent an alternative habitat for some threatened species, particularly if those species have the behavioural adaptations required for survival in a production landscape and if wildlife-friendly farming practices are used. In order to encourage these species into such landscapes, it is possible to use reintroduction methods to release individuals into target areas. However, prior to the reintroduction of New Zealand falcons into vineyards, no avian reintroductions in New Zealand, to my knowledge, have focused on releasing a threatened species into an agricultural region.

The main goal of a reintroduction project should be to establish a self-sustaining breeding population of the focal species. Despite the popularity of this rather expensive and management-intensive technique, the majority of reintroduction projects either fail to achieve this goal or have unknown results due to a lack of monitoring (Fischer & Lindenmayer 2000). Reintroduction projects that release a large number of individuals (> 100), that use a wild source population, and that have removed the initial cause of decline are more likely to succeed (Fisher & Lindenmayer 2000).

Successful reintroduction programmes are reliant upon incorporating the behavioural and physical requirements of the species in question into reintroduction strategies (Knight 2001; Blumstein & Fernández-Juricic 2004; Berger-Tal et al. 2011). In many cases, individuals released as part of a reintroduction programme are unable to display natural behaviour and this can have dire consequences for the success of the programme (Blumstein & Fernández-Juricic 2004). The need to assess the behavioural ramifications of translocation is vital, as released individuals can have lower survival rates than wild-reared counterparts (Brown et al. 2006; Aaltonen et al. 2009; Reid et al. 2010). This is particularly acute when animals are reintroduced into anthropogenic landscapes.

Here I seek to determine whether the active conservation of New Zealand falcons in agricultural land is mutually beneficial to farmers and to conservationists. The first facet of Falcons for Grapes (FFG), the efficacy of falcons as biological control agents of passerine pest species is addressed in Chapter 2, where I use a combination of pest bird abundance counts and grape damage surveys to quantify the effect of falcon presence on these economically important factors. The second facet of FFG, the efficacy of the reintroduction programme as a conservation tool for falcons is less straightforward to measure, and the remainder of my thesis focuses on comparing multiple components of falcon behaviour and habitat characteristics in the hills and vineyards, each of which has implications for the survival and productivity of falcons. In Chapter 3, I introduce a remote videography system that I developed in order to monitor the behaviour of nesting falcons that was used to collect the data for chapters 4, 5, and 7. In Chapter 4, I use prey abundance counts and a study of falcon diet during the breeding season to determine if falcons have access to the same food species in vineyards as they do in hills, to determine if falcons select for or against any specific prey species, and to give the most complete picture of falcon diet produced to date. In Chapter 5, I focus on whether the move from unmanaged hill habitat to vineyard habitat has changed the breeding behaviour and feeding rates of nesting falcons, and provide detailed information on the breeding habits of this threatened species. Chapter 6 compares the behavioural development of juvenile falcons that have been released as part of the reintroduction scheme, and therefore do not undergo training by adult falcons, with the behavioural development of juvenile falcons raised by their parents in wild nests. Finally, in Chapter 7, I use an artificial nest experiment to compare nest predation rates and potential nest predators between the two habitats. In Chapter 8, I discuss the implications of this research for future conservation of New Zealand falcons, as well as for the link between vertebrate predators and agricultural landscapes.

CHAPTER TWO

EFFECTS OF INTRODUCING THREATENED FALCONS INTO VINEYARDS ON ABUNDANCE OF PASSERINE BIRDS AND GRAPE YIELD

Two juvenile falcons stand guard in a vineyard (Photo: S. Kross)

Kross, S.M., Tylianakis, J.M., & Nelson, X.J. 2012. Effects of Introducing Threatened Falcons into Vineyards on Abundance of Passeriformes and Bird Damage to Grapes. *Conservation Biology*. 26: 142-149. doi: 10.1111/j.1523-1739.2011.01756.x

ABSTRACT

Agricultural landscapes are becoming an important focus of animal conservation, although predator conservation initiatives to date have rarely provided economic benefits to agricultural producers. We examined whether introduction into vineyards of the New Zealand Falcon (*Falco novaeseelandiae*), a species listed as threatened by the New Zealand Department of Conservation, was associated with changes in the abundance of four species of passerine birds that are considered to be vineyard pests, and with changes in the economic costs of grape damage. Three introduced species, the blackbird (*Turdus merula*), song thrush (*Turdus philomelos*), and starling (*Sturnus vulgaris*), remove whole grapes from bunches whereas one native species, the silvereye (*Zosterops lateralis*), pecks holes in grapes. We found that the introduction of falcons to vineyards was associated with a significant decrease in the number of introduced passerines, and with a 95% reduction in the number of grapes removed, compared to vineyards without falcons. Falcon presence was not associated with a change in the number of silvereyes, but there was a 55% reduction in the number of grapes pecked in falcon vineyards. Our results indicate that, relative to damage in vineyards without falcons, the presence of a falcon could potentially result in savings of USD 233 / ha for Sauvignon Blanc grapes and USD 326 / ha for Pinot Noir grapes.

INTRODUCTION

Conservation has traditionally been viewed as a separate endeavour from agriculture (Green et al. 2005; Perrings et al. 2006). However, recently ecologists have examined whether biological control of pests may provide an incentive for the conservation of certain species within agricultural systems (Daily et al. 2000; Tilman et al. 2002). Conservation of predators can be a successful and sustainable approach for the control of many insects considered to be pests. Therefore, substantial research has focused on the management of habitats of predatory arthropods that reduce the abundance of arthropod pests (Chiverton & Sotherton 1991; Landis et al. 2000). Efforts to augment natural populations of predatory arthropods often represent additional costs to landowners, because land is taken out of production or yields are reduced (Green et al. 2005; Foley et al. 2005), and the predators themselves are seldom classified as threatened by conservation organizations. The ability of vertebrates to control arthropod agricultural pests has received much less attention, despite evidence that predators such as birds and lizards can effectively reduce damage to agricultural crops caused by their prey (Borkhataria et al. 2006; Kellermann et al. 2008). Moreover, when the agricultural pests themselves are vertebrates, control methods rarely focus on the preservation of natural predators, because the predators of vertebrates tend to be large, carnivorous species that are difficult to contain and rarely specialize on a single prey species (Hoddle 1999).

Vineyards are particularly vulnerable to predation by Passeriformes, because ripening grapes (*Vitis vinifera*) represent an abundant food source for these birds in late summer and autumn (Somers & Morris 2002; Tracey & Saunders 2003; Saxton et al. 2004). For example, in Marlborough, New Zealand's largest wine-growing region, three species of introduced European birds, blackbirds (*Turdus merula*), song thrushes (*Turdus philomelos),* and starlings (*Sturnus vulgaris*), remove whole grapes from bunches, whereas the native silvereye (*Zosterops lateralis*) pecks holes in grapes to drink the juice from within, exposing the grapes to fungal infection (Tracey & Saunders 2003; Saxton et al. 2004). Starlings, blackbirds and song thrushes are also known dispersers of non-native invasive fruiting plants (Williams & Karl 1996).

In order to mitigate grape damage, viticulturalists employ a variety of bird-deterrent methods, including acoustic, physical, and lethal techniques. However, commercial deterrents are often expensive, their efficacy may be exaggerated by advertisers (Fukuda et al. 2008), and

some methods may even increase the amount of damage to grapes (Bomford & Sinclair 2002). Furthermore, even when physical or acoustic deterrents are used, birds can damage up to 83% of a vineyard's crop (Tracey & Saunders 2003).

Trained falcons are sometimes used to remove avian pests from areas such as airports and landfills (Baxter & Allan 2006; Soldatini et al. 2008), and artificial perches (Kay et al. 1994; Wolff et al. 1999) and nest boxes (Meyrom et al. 2009) have been used to attract wild birds of prey into some agricultural areas in order to reduce the abundance of rodents. These efforts demonstrate that captive or wild birds of prey are capable of reducing pest abundance. Using the New Zealand falcon (*Falco novaeseelandiae*) as a case study, we compared the abundance of birds considered to be pests and levels of grape damage in vineyards with resident falcons (introduced for conservation) with those in control vineyards.

METHODS

Falcon introduction

Falco novaeseelandiae is the country's only remaining endemic bird of prey. The population size and distribution of falcons decreased considerably after the arrival of human settlers (Fox 1977; Gaze & Hutzler 2004), and the species is now classified as threatened by the New Zealand Department of Conservation (Miskelly et al. 2008). The Falcons For Grapes (FFG) project has been relocating wild New Zealand Falcon chicks from their nests in the mountains to the vineyards of Marlborough since 2005 (Fox 2005). No falcons, or other passerine-hunting raptors, occurred in this region prior to the relocations. Relocated falcons are provided with supplementary food and their nests are protected from mammalian predators. There are no *a priori* criteria for selection of vineyards into which falcons are introduced.

We selected 6 vineyards in which falcons had been introduced (*falcon vineyards*) and 6 vineyards in which falcons had not been introduced (*control vineyards*). Treated and control vineyards were interspersed spatially, and edges of vineyards were a minimum of 4 km apart (Fig. 2.1). All vineyards were managed using common commercial (not organic) methods for spatially extensive viticulture that were approved by Sustainable Winegrowing New Zealand.

We trained workers in control vineyards in falcon identification and asked them to report any falcon sightings over the 2 years of the study.

Vineyards were considered to be falcon vineyards if at least one falcon was being fed with supplementary food at least five times per week within the vineyard over the grape ripening period. This guarantees that falcons were active and flying within the vineyard (in order to receive food) during the time that pest birds would be feeding on grapes. Falcons were also documented to prey upon all four of the pest bird species throughout the study (Chapter 3).

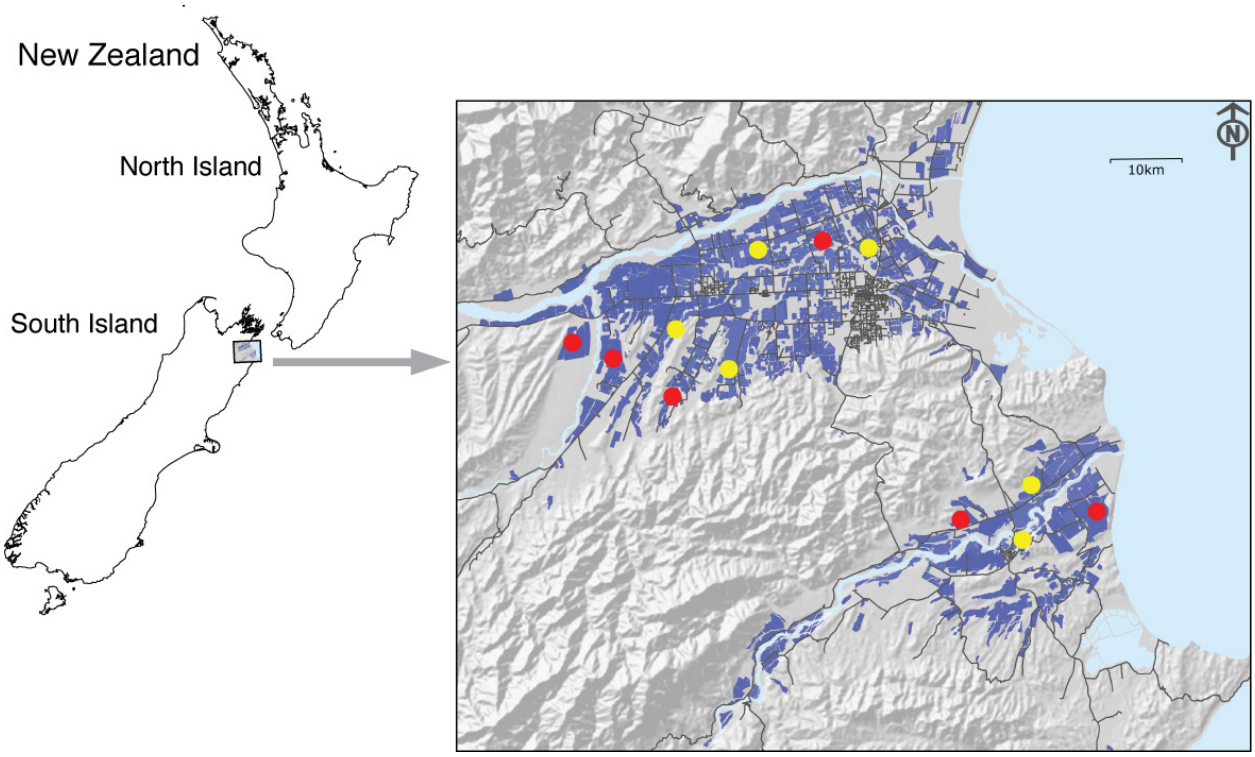

Figure 2.1. Map of the wine-growing valleys of Marlborough. Vineyards are marked in dark blue, the upper patch of vineyards shows the Wairau Valley, while the lower patch shows the Awatere valley. Mountains are shown in greyscale, and roads are black lines (residential areas such as towns are shown as densely drawn black lines). Vineyards with falcons are shown as red circles, control vineyards without falcons are shown as yellow circles. (Map courtesy of Wine Marlborough Ltd.).

Vineyard characteristics

Marlborough's vineyards are located at the northeastern part of New Zealand's South island, in the Wairau Valley, near the town of Renwick (41°30'S, 173°50'E), and in the Awatere Valley, near the town of Seddon (41°40'S, 174°04'E). Sauvignon Blanc is the dominant variety of wine grape (21.5 ± 4.43 ha/vineyard), and Pinot Noir is the second-most common (3.3 ± 4.52 ha/vineyard, MAF 2009a). The vineyards we studied had 49.3 ± 10.4 ha of Sauvignon Blanc

grapes and 13.0 ± 4.8 ha of Pinot Noir grapes. Falcon vineyards had 73.19 ± 38.99 ha of Sauvignon Blanc, and 22.5 ± 8.5 ha of Pinot Noir, and control vineyards had 40.68 ± 12.44 ha of Sauvignon Blanc, and 6.67 ± 1.67 ha of Pinot Noir. The average area covered by each grape variety did not differ significantly between vineyards with- and without- introduced falcons (using *student's t*-test to test between control and falcon vineyards for each variety: $p = 0.442$ for Sauvignon Blanc, and $p = 0.305$ for Pinot Noir).

Vineyards with falcons and control vineyards were similar in environmental features. All had analogous edge habitat features that were dominated by non-native plant species such as grasses, *Pinus radiata*, *Populus nigra*, *Salix fragilis*, *Cytisus scoparius*, and *Eucalyptus globulus*. These were intermixed sparsely with common native species such as *Cordyline australis* and *Leptospermum scoparium*.

Birds feed on grapes primarily at vineyard edges, nearest to vegetation or structures that provide passerines with shelter from potential predators. Feeding decreases toward the centre of the vineyard (Somers & Morris 2002). However, starlings in Europe and Australia have been observed to feed toward the centre of agricultural fields, in areas further away from shelter, because the open space may better accommodate their antipredator behaviour (Whitehead et al. 1995; Tracey & Saunders 2003). Birds are known to flee from vineyards when approached by potential predators, and grapevines are unlikely to provide shelter for birds (Laiolo 2005). We therefore classified sampled vines as either *edge* or *interior* to account for differences in distance to vegetation (from long grasses to dense trees) in which passerines could take shelter from predators (bird shelter). We considered 50 m the threshold between interior and edge because in discussions with experienced vineyard managers before the onset of data collection we learned that the majority of damage in the previous 5 years occurred within 50 m of bird shelter. The mean percentage of edge compared with interior of the sampled area was 27.3 ± 4.2% for Sauvignon Blanc and 33.0 ± 6.2% for Pinot Noir.

Abundance of Passeriformes

We established 1 edge and 1 interior transect within each of 4 falcon vineyards and 4 control vineyards. Transects were 500 m long and a minimum of 150 m away from centre transect lines to avoid sampling the same individuals within both interior and edge transects. Because the

edge transect ran alongside bird shelter, we used one-sided transect methods (Bibby et al. 2000). We walked each transect in one direction for 20 minutes and, using field binoculars (15 x 50 IS), identified all Passeriformes seen within 50 m of the transect line, including the 4 focus pest species (introduced blackbirds, song thrushes and starlings and the native silvereye) and 11 other common non-pest species. We ignored birds flying overhead. All transects ran along the edges of blocks, perpendicular to the rows of grapes. The number of individuals of each bird species observed during each survey of a transect was recorded; we refer to these counts as *abundance data*. We collected abundance data at 6 of the vineyards (3 falcon and 3 control) once a week starting the week of 23 November 2008 and at 2 of the vineyards (1 falcon and 1 control) once a week starting the week of 1 January 2009. We surveyed until the week of 18 March 2009, which was immediately prior to the start of the grape harvest. We analysed each sample (transect survey) separately, but time (week) was included as a factor to control for temporal effects and vineyard was included to control for nonindependence of samples from multiple visits (see Analyses). We collected abundance data along transects between 06:00 and 10:00 and did not collect data when winds were high, temperatures were hot, or rain was moderate to heavy. If conditions precluded sampling, we sampled the transect during the same week under better conditions.

Grape damage

In 2009 we measured grape damage (Fig. 2.2) in the 8 vineyards in which we conducted bird abundance surveys. In 2010 we again sampled 3 of the vineyards with falcons and 3 of the control vineyards from 2009, with the addition of 2 recently established falcon vineyards and 2 new control vineyards. One vineyard contained falcons in 2009 but not in 2010, so we treated it as a falcon vineyard in 2009 and as a control in 2010.

We sampled grape damage in the weeks of 18 March 2009 and 22 March 2010, which were immediately prior to the onset of harvest. Therefore, we used damage recorded during this period to estimate economic loss. We split vineyards into a grid of 50 x 50 m sampling plots and randomly selected a minimum of 10 edge and 10 interior plots for sampling in each vineyard (Fig 2.3). Each plot contained only one variety of grapes. The few rows that were covered in bird-exclusion netting were not sampled. We sampled 1 grape bunch from each of

10 vines within each plot. We sampled 5 vines on each side of a row approximately midway along the plot at the edge nearest bird shelter. Sampling vines on both sides of the row controlled for differences in sunlight exposure.

We selected grape bunches for sampling with a method we adapted from Saxton (2006) that ensures a random selection of bunches from locations within and outside the vine canopy (Fig. 2.4). We estimated, to the nearest 5 grapes, the total number of grapes that had not been pecked or removed (undamaged grapes), the number of grapes that had been pecked, and the number of stems (pedicels) indicating grapes had been removed (Fig. 2.2). We sampled 750 and 1490 bunches in control vineyards and 850 and 1050 bunches in vineyards with falcons in 2009 and 2010, respectively.

Figure 2.2. Examples of grape bunches that have been damaged by bird foraging. a) Pinot Noir bunch with recent pecking. b) Pinot Noir bunch with removed grapes. c) Sauvignon Blanc bunch with all grapes removed. d) Sauvignon Blanc bunch with pecked grapes that have a fungal infection.

Figure 2.3. Map showing one vineyard that was used in our study. The sections of vineyard growing Sauvignon Blanc (non-Sauvignon Blanc varieties are filled in with cross-hatching and were not included in our study) have been split into edge or interior types, with the edge plots highlighted in yellow. 50 x 50m plots were drawn onto the map using a ruler, and each plot was assigned a sequential number. The edge and interior plots were numbered separately, and then a selection of random numbers from the available numbers was generated for both edge and interior types. When the vineyard was visited, these plots were visited in the order drawn from the random number sequence. Plots sampled are marked with red circles. Within each plot, the row closest to the edge of the vineyard was sampled, and 10 vines were sampled from alternating sides of the row. The map also contains information about the habitat types at this vineyard: light green lines show small trees; dark green lines show large trees; blue represents water; and orange represents pasture.

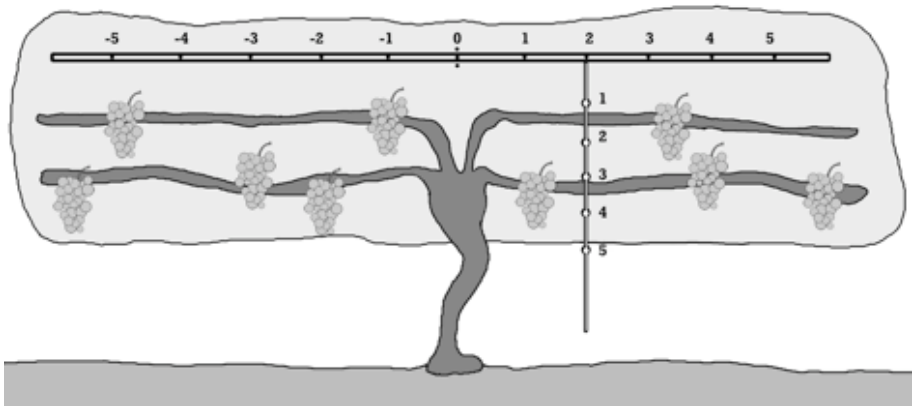

Fig. 2.4. Method used to randomly sample grape bunches for damage assessment. Adapted from Saxton (2006) and Tracey and Saunders (2003). A one-meter long bamboo pole was marked with eleven notches, each 10cm apart, numbered from -5 to +5. For each grape vine, the pole was held horizontally at a height approximately 10cm above the highest grape bunch, with the '0' notch directly above the trunk of the vine. Five knots, labelled one to five, were tied onto a string at 10cm intervals and that string was hung from the pole so that it could be slid from notch to notch. A list of random pairs of numbers, the first representing the notch on the pole and the second representing the knot on the string, was used to choose the location on the vine from which to sample. The bunch closest to the chosen location was sampled, and, if no bunch was present, a new sequence of pole-string locations was chosen. These methods ensure a random selection of bunches from all locations on vines and from both within and outside of the vine canopy (Saxton 2006).

We measured the cardinal direction each bunch faced and visually estimated the level of canopy cover for each bunch: 0, bunches with no canopy cover; 1, bunches with >0-50% canopy cover; 2, bunches with >50-100% canopy cover. From the edge of each plot, we measured the distance to the nearest bird shelter. If that bird shelter was located within 50 m of the sampled plot, we also characterized the type of shelter according to presence or absence of grasses, shrubs, small trees (< 3 m in height), large trees (≥ 3 m in height), buildings, and water. We used a scale from 0 to 5 to quantify the bird-scaring methods applied to each vineyard each year: 0, no bird-scaring methods; 1, only static nonacoustic methods (e.g., kites, balloons, ribbon); 2, static acoustic methods (gas cannons or avian alarm calls) set to go off every 5-10 minutes between dawn and dusk and rarely (1-2 times per week) deployed mobile acoustic methods (workers on 4-wheeled bikes or in vehicles honking horns or activating mobile gas cannons); 3, moderately deployed (once per day) mobile acoustic or lethal (workers with shotguns) methods; 4, often-deployed static nonacoustic methods and mobile acoustic and lethal methods (3-4 times daily); and 5, continuous mobile acoustic and lethal methods throughout daylight hours.

Analyses

Passeriforme abundance was the number of individuals of each focal species counted in each vineyard per week. We used generalised linear mixed models (GLMMs) with a Poisson error, the most appropriate distribution for count data, and a log-link function to analyse the associations among abundance of focal species, weekly variability of focal species' presence, falcon presence, and location of the transect (interior versus edge). We used the lme4 package (Bates et al. 2008) in R (version 2.7.2) for the GLMMs (R Core Development Team 2008). Mixed-effects models allow the inclusion of grouping (random) factors to account for nonindependence of data in nested and split-plot designs. We included vineyard as a random effect (so that multiple samples within one vineyard were not treated as independent) and week, falcon presence, and transect location as fixed factors, with interaction terms included among all 3 fixed factors in the maximal models. The GLMMs incorporated our hierarchical design and tested the effect of falcon presence over an error term, with degrees of freedom derived from number of vineyards. For transect location (edge versus interior) error degrees of freedom were derived from the number of transects (but blocked according to vineyards). We simplified the maximal models by removing interactions then main effects until no further reduction in residual deviance (measured using Akaike's information criterion) was obtained.

For the grape-damage data, we used a principal components analysis (PCA) to reduce the number of variables characterizing bird shelter to the 4 orthogonal axes that each explained more than 10% of the variance and cumulatively explained 86.7% of the variance in these variables (Table 2.3). We then used GLMMs with a binomial error and a logit-link function to test whether falcon presence, canopy cover, grape variety, vineyard bird-scaring effort, distance from nearest bird shelter, cardinal direction the bunch faced, the 4 PCA axes, and plot location were significantly associated with the proportion of grapes per bunch (bunches being the unit of replication) that were damaged. We used separate models to test each of our damage categories: proportion of grapes per bunch removed but not pecked (removed) and proportion of grapes per bunch pecked but not removed (pecked). We included vineyard, plot, and year as random effects; plot nested within vineyard accounted for nonindependence of bunches within plots and of plots within vineyards and potential variation in damage across years. We initially included

up to as many as 4 interaction terms between combinations of all available predictor variables and then reduced the maximal model to the minimum adequate model with the procedure outlined above. We tested all models for evidence of overdispersion (on the basis of ratio of residual deviance to degrees of freedom) and reanalysed overdispersed models with generalised linear mixed models fitted with penalized quasi likelihood (the 'glmmPQL' function) in the MASS package (Venables & Ripley 2002) in R. We used the parameter estimates from each model (after applying an appropriate inverse-link function) to estimate the actual abundance of birds or proportion of grapes removed or pecked.

Relationship between bird abundance and grape damage

Because we measured pest bird abundance at the scale of the entire vineyard rather than at the plot-level (as grape damage was), we compared the cumulative pest bird abundance over the final five weeks of grape ripening in 2009, with overall average plot damage in each vineyard in that year using Spearman correlations. We performed correlations for each of overall damage, pecked damage, and removed damage for all pest species combined, then separately for native silvereyes and for a combined 'introduced' category including blackbirds, song thrushes and starlings.

Economic effect

We estimated the economic effect of falcon presence in vineyards by combining a GLMM of overall grape-damage (the sum of pecked and removed grapes) in vineyards with falcons and control vineyards with average value of grapes harvested per hectare. In the overall grape-damage model, we used the same analysis methods as above for each damage class. In 2009 the average gross purchase price of grapes in Marlborough was US $13,790 ± 430/ha for Sauvignon Blanc (assuming a conversion rate of 1NZ $= US $0.718) and $13,951 ± 738/ha for Pinot Noir grapes (MAF 2009a).

RESULTS

Bird abundance

Workers in vineyards without falcons reported no falcon sightings over the 2 years of our study. After controlling for differences through time, falcon presence in vineyards was associated with a 78.4% reduction in the abundance of song thrushes ($Z = -3.17$, $p < 0.01$), an 82.5% reduction in the abundance of blackbirds ($Z = -2.44$, $p = 0.02$), and a 79.2% (nonsignificant) reduction in the abundance of starlings ($Z = -1.85$, $p = 0.06$) (Fig. 2.5) relative to control vineyards. Falcon presence did not explain significant variation in silvereye abundance ($Z= -1.03$, $p = 0.30$) (Fig. 2.5), so we removed this variable from the silvereye model; the lack of effect may have been due to low power.

Interior vines were associated with 70.5% fewer song thrushes ($Z = -7.66$, $p < 0.001$), 95.2% fewer silvereyes ($Z = -10.71$, $p < 0.001$), and 44.4% fewer blackbirds ($Z = -1.83$, $p = 0.07$) relative to edge vines. Conversely, interior vines were associated with a 57.7% increase in starlings ($Z = 3.33$, $p = 0.001$) relative to edge vines.

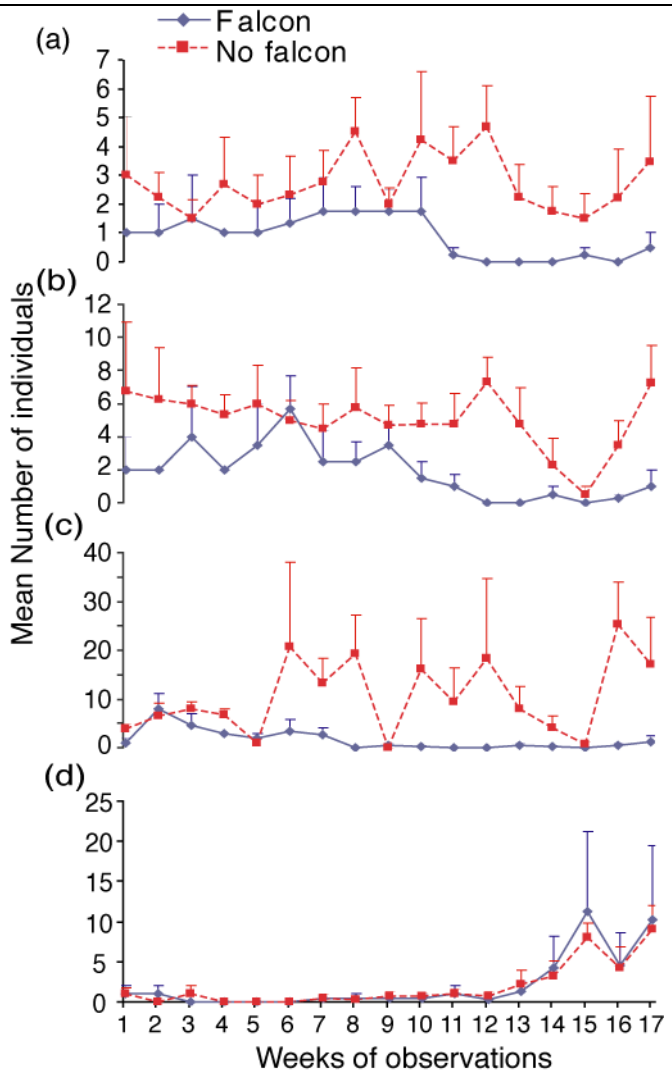

Figure. 2.5. The effects of falcon presence on the abundance of (a) song thrushes ($p < 0.01$), (b) blackbirds ($p = 0.02$), (c) starlings ($p = 0.06$), and (d) silvereyes ($p = 0.30$, removed from model). Line graphs show the mean (+ S.E.M.) number of individuals observed in each of 17 weeks (beginning the week of 23 November 2008 and ending the week of 18 March 2009) along edge and interior transects combined at 4 vineyards with resident falcons present (Falcon) and 4 vineyards with falcons absent (No falcon). Grape ripening began at approximately week 12.

Grape damage

There was significantly less grape damage in vineyards with falcons than in control vineyards for edge and interior Sauvignon Blanc and Pinot Noir bunches (Fig. 2.6). Results of the generalised linear mixed models showed that in vineyards with falcons present there were significantly fewer grapes removed from bunches ($p < 0.001$) and fewer grapes pecked on bunches ($p < 0.01$; Appendix 1). With all other variables held constant, the model intercept

(inverse linked) indicated that in control vineyards an average of 0.6% of the edge Sauvignon Blanc grapes were removed and 2.3% were pecked (Table 2.1). In contrast, vineyards with falcons had an average of 0.03% of edge Sauvignon Blanc grapes removed and 1.0% pecked (Table 2.1).

Canopy cover was associated with observed damage to grapes. In control vineyards, bunches with >0-50% canopy cover had 43.3% fewer grapes removed ($p < 0.001$) than bunches with no canopy cover, whereas grape bunches with >50-100% cover had 89.4% fewer grapes removed and 47.0% fewer pecked grapes (both $p < 0.001$; Table 2.2) than bunches with no canopy cover. However, in vineyards in which falcons were present, 32.5% more grapes were removed ($p < 0.001$) in bunches with >0-50% cover than in bunches with no canopy cover (Table 2.2).

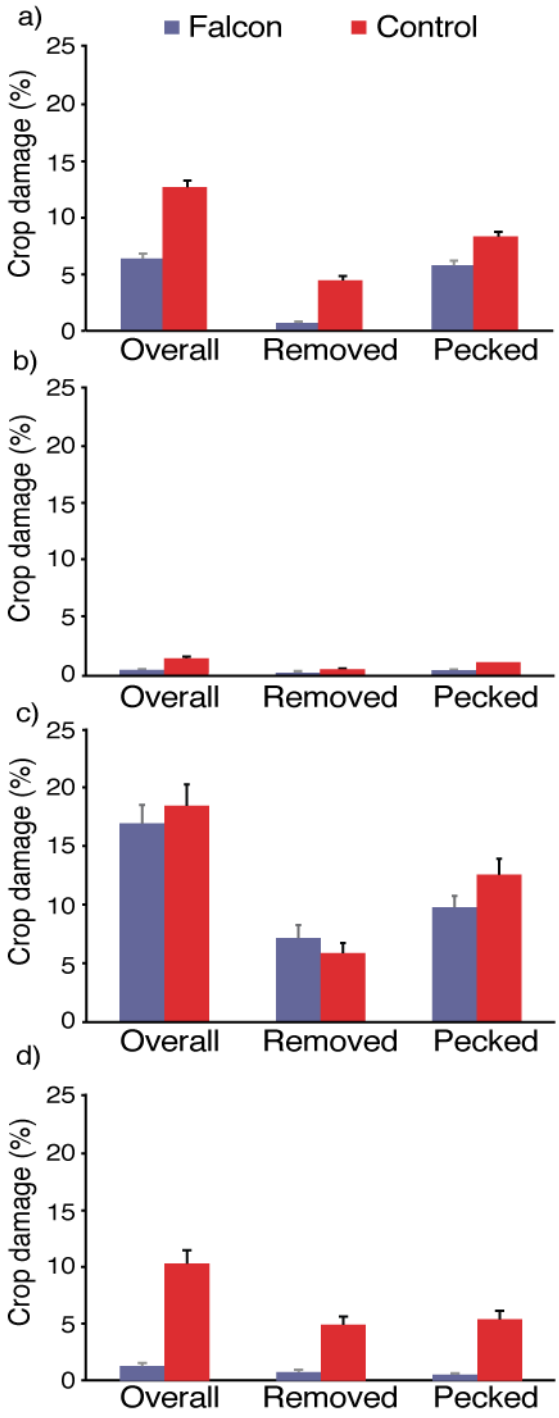

Figure. 2.6. Mean (+ S.E.M.) percent overall-damage to grapes (removed and pecked combined), grapes removed, and pecked grapes in falcon and control vineyards for (a) edge Sauvignon Blanc (b) interior Sauvignon Blanc, (c) edge Pinot Noir, and (d) interior Pinot Noir.

Table 2.1. Mean percent damage per bunch to vineyard grapes due to passerine foraging in control vineyards and in vineyards containing resident falcons, calculated from inverse-linked parameter estimates from generalised linear mixed models for removed and pecked grapes.

Damage, grape type, location*	Control (% damage)	Falcon (% damage)	Relative change in damage with falcon presence (%)
Grapes removed			
Sauvignon Blanc			
Edge	0.62	0.03	-95.8
Interior	0.03	0.00	-99.0
Whole vineyard	0.19	0.01	-95.4
Pinot Noir			
Edge	1.12	0.05	-95.8
Interior	0.06	0.00	-95.8
Whole vineyard	0.35	0.01	-95.8
Grapes pecked			
Sauvignon Blanc			
Edge	2.26	1.00	-55.6
Interior	1.05	0.46	-55.9
Whole vineyard	1.38	0.61	-56.0
Pinot Noir			
Edge	3.50	1.57	-55.3
Interior	1.65	0.73	-55.8
Whole vineyard	2.15	0.95	-55.6

*Whole vineyard damage was calculated as the amount of edge-damage multiplied by the proportion of control and treatment vineyards that consisted of edge vines (Sauvignon Blanc = 27%, Pinot Noir = 33%) plus the amount of interior-damage multiplied by the proportion of our control and treatment vineyards that consisted of interior vines.

Table 2.2. Summary of variables retained in the models for removed damage and pecked damage.

	Removed Damage				Pecked Damage			
	Estimate	SE	Z value	*p*	Estimate	SE	Z value	*p*
(Intercept)	-5.067	0.284	-17.822	<0.001	-3.769	0.237	-15.882	<0.001
Falcon Present	-3.176	0.420	-7.557	<0.001	-0.825	0.275	-3.005	0.003
Interior Vines	-2.904	0.547	-5.308	<0.001	-0.775	0.320	-2.423	0.015
Pinot Noir	0.590	0.656	0.900	0.368	0.453	0.456	0.995	0.320
Half canopy	-0.570	0.054	-10.570	<0.001	0.025	0.038	0.664	0.506
Full Canopy	-2.253	0.116	-19.458	<0.001	-0.647	0.053	-12.158	<0.001
Bird Scaring 1-5	Removed from simplified model				Removed from simplified model			
Direction (north)	0.573	0.412	1.391	0.164	0.246	0.300	0.819	0.413
Direction (south)	-0.171	0.418	-0.408	0.683	-0.002	0.301	-0.007	0.995
Direction (west)	0.206	0.037	5.586	<0.001	-0.063	0.023	-2.762	0.006
Distance from bird shelter (m)	Removed from simplified model				-0.002	0.001	-2.022	0.043
PCA 1	-0.611	0.130	-4.713	<0.001	-0.599	0.080	-7.529	<0.001
PCA 2	Removed from simplified model				0.154	0.081	1.910	0.056
PCA 3	0.463	0.146	3.163	0.002	0.233	0.088	2.656	0.008
Falcon present: Interior vines	1.765	0.984	1.794	0.073	-0.372	0.334	-1.114	0.265
Falcon present: Pinot Noir	2.235	0.877	2.548	0.011	0.270	0.609	0.444	0.657
Interior vines: Pinot Noir	4.205	0.957	4.394	<0.001	Removed from simplified model			
Falcon present: Half canopy	0.852	0.190	4.475	<0.001	-0.094	0.056	-1.698	0.089
Falcon present: Full canopy	0.734	0.370	1.985	0.047	-0.440	0.083	-5.271	<0.001
Interior vines: Half canopy	1.304	0.153	8.493	<0.001	0.332	0.085	3.923	<0.001
Interior vines: Full canopy	1.457	0.389	3.744	<0.001	-0.592	0.176	-3.367	<0.001
Pinot Noir: Half canopy	-0.309	0.114	-2.715	0.007	Removed from simplified model			
Pinot Noir: Full canopy	0.763	0.307	2.485	0.013	Removed from simplified model			

	Removed Damage				Pecked Damage			
	Estimate	SE	Z value	*p*	Estimate	SE	Z value	*p*
Falcon Present: Interior vines: Pinot Noir	-2.895	1.477	-1.96	0.050	Removed from simplified model			
Falcon Present: Interior vines: Half canopy	-1.968	0.359	-5.487	<0.001	Removed from simplified model			
Falcon Present: Interior vine: Full canopy	-0.538	0.815	-0.661	0.509	Removed from simplified model			
Falcon present: Pinot Noir: Half canopy	-0.299	0.237	-1.259	0.208	Removed from simplified model			
Falcon present: Pinot Noir: Full canopy	-1.904	0.607	-3.137	0.002	Removed from simplified model			
Interior vines: Pinot Noir: Half canopy	Removed from simplified model				Removed from simplified model			
Interior vines: Pinot Noir: full canopy	Removed from simplified model				Removed from simplified model			
Falcon present: Interior vines: Pinot Noir: Half canopy	Removed from simplified model				Removed from simplified model			
Falcon present: Interior vines: Pinot Noir: Full canopy	Removed from simplified model				Removed from simplified model			

(The intercept represents sites with no falcon present, edge vines, Sauvignon Blanc variety, no canopy cover, east-facing vines, no bird scaring, no PCA input and 0m from nearest bird shelter. Colons (:) between two terms represent an interaction effect within the model, Table 2.3 shows the makeup of each PCA axis. Each type of damage was modelled independently using generalised linear mixed models with binomial errors and a logit link function, and simplified using AIC. To convert the estimates to true proportions the values need to be inverse-linked ($e^{\eta} / (1 + e^{\eta})$) as we have done in Table 2.1.)

Distance from bird shelter had a significant negative association with the number of grapes pecked (0.02 % damage, $p = 0.04$), but this variable was taken out of the removed-damage model (Table 2.2). Bunches within the vineyard interior had significantly fewer grapes removed (0.03 %, $p < 0.001$) and pecked grapes (1.0 %, $p = 0.02$) than bunches at the edge of the vineyard (Table 2.2). Principal component axis 1, which was negatively correlated with the presence of natural features such as shrubs (variable loading = - 0.54), small trees (- 0.46), large trees (- 0.43), and water (- 0.44; Table 2.3), had a significant negative association with both damage categories (both $p < 0.001$; Table 2.3). Principal component axis 2 was positively correlated with the presence of buildings (0.95; Table 2.3) and had a nonsignificant positive association with pecked damage ($p = 0.06$), but we took this variable out of the removed-damage model during simplification (Table 2.2). Principal component axis 3 was negatively correlated with the presence of water (- 0.53; Table 2.3) and had a significant positive association with removed and pecked damage (both $p < 0.01$; Table 2.2). We removed principle components axis 4 and level of bird scaring in vineyards from the removed- and pecked-damage models during simplification.

Table 2.3. Correlations between the original bird shelter habitat variables (measured in presence or absence) and the first four axes from a principle components analysis (PCA) which were included as variates in the grape damage analysis.

Habitat variables	Axis 1	Axis 2	Axis 3	Axis 4
Grasses	-0.342	-0.101	0.812	-0.320
Shrubs	-0.537	-0.145	0.091	0.245
Small trees (<3m)	-0.458	-0.038	-0.021	0.667
Large trees (>3m)	-0.427	0.241	-0.218	-0.568
Water	-0.441	-0.129	-0.526	-0.221
Buildings	-0.089	0.945	0.083	0.145
Standard Deviation	1.585	1.017	0.930	0.887
Proportion of variance	0.419	0.172	0.144	0.131
Cumulative proportion	0.419	0.591	0.735	0.867

In the vineyard in which falcons were present in 2009 and absent in 2010, damage was lower in 2009 (mean damage = 2.0 ± 0.5%) than in 2010 (5.2 ± 1.0%), whereas the remaining vineyards showed no significant between-year difference (Fig. 2.7).

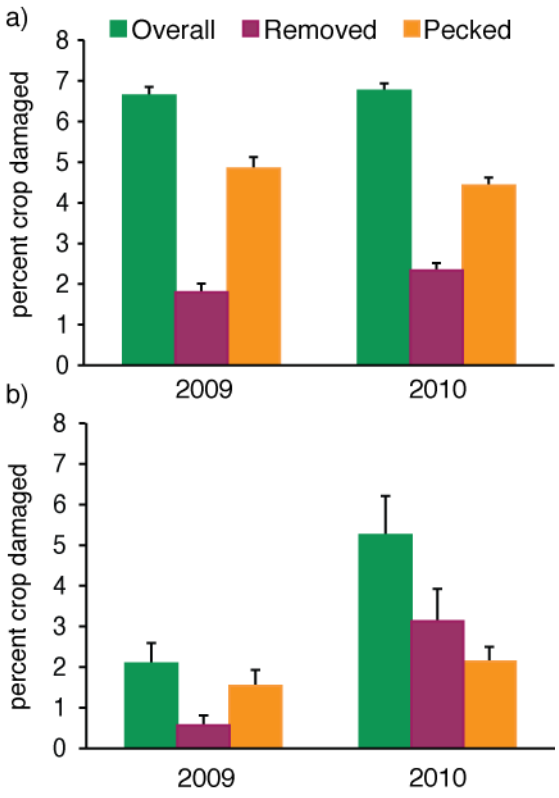

Figure 2.7. Mean (+S.E.M.) percent of overall, removed, and pecked damage for edge Sauvignon Blanc over two years of grape damage sampling in a) all vineyards combined; and b) a vineyard with falcons in 2009 and without falcons in 2010.

Relationship between bird abundance and grape damage

The number of grapes removed in each vineyard was correlated with the cumulative number of blackbirds, song thrushes and starlings (rho = 0.536, p = 0.032), but not with the cumulative number of silvereyes (rho = 0.345, p = 0.191). In contrast, pecking damage was highly correlated with the cumulative number of silvereyes (rho = 0.722, p = 0.002), but not with the cumulative number of blackbirds, song thrushes and starlings (rho = 0.364, p = 0.112). The overall amount of damage recorded in each vineyard was strongly correlated with the cumulative number of silvereyes observed in each vineyard (rho = 0.583, p = 0.018), but not with the cumulative number of blackbirds, song thrushes and starlings (rho = 0.412, p = 0.112).

Economic effect

For the combined average overall damage from both pecked and removed damage, 2.45% of the Sauvignon Blanc crop and 3.54% of the Pinot Noir crop in control vineyards was damaged by birds (Table 2.4), equivalent to losses of $338/ha and $481/ha, respectively. A mean of 0.76% of the Sauvignon Blanc crop and 1.11% of the Pinot Noir crop was damaged in vineyards with falcons (Table 2.4), equivalent to losses of $104/ha and $155/ha, respectively.

Table 2.4. Mean percent overall damage (pecked and removed damage combined) per bunch to vineyard grapes (SB: Sauvignon Blanc, PN: Pinot Noir) due to pest bird foraging in control vineyards and in vineyards containing resident falcons, calculated from inverse-linked parameter estimates from a penalised quasi-likelihood GLMM

Grape type, location	Control (% damage)	Falcon (% damage)	Relative % change in damage due to falcon presence
Sauvignon Blanc			
Edge	5.46	1.71	-68.7
Interior	1.34	0.41	-69.6
Whole vineyard	2.45	0.76	-69.0
Pinot Noir			
Edge	7.12	2.26	-68.1
Interior	1.77	0.54	-69.5
Whole vineyard	3.54	1.11	-68.6

(Whole vineyard damage was calculated using the edge and interior damage results and taking into account the proportion of our focal vineyards that consisted of edge vines (SB = 27%, PN = 33%). The summary of variable retained in the overall damage models is given in Appendix 1).

DISCUSSION

Our results show that relative to vineyards without falcons, vineyards with falcons were associated with significantly fewer non-native focal passerines and significantly fewer pecked and removed grapes. Relative to vineyards without falcons, falcon presence was associated with $233/ha less crop damage for Sauvignon Blanc and $326/ha less damage for Pinot Noir. Because these are rough calculations derived from model estimates, the values should not be treated as exact. Not only can these findings be incorporated into avian pest management in viticulture and in other agricultural sectors, but they demonstrate that raptor conservation and biological control are mutually compatible goals. This potential benefit of falcon presence for avian pest control is not limited to vineyards; bird damage is also a problem for fruit and arable

crop industries in New Zealand and globally (Kozicky and McCabe 1970; Ward et al. 1979; Coleman and Spurr 2001; Bomford and Sinclair 2002). Therefore, it may also be beneficial for farmers to encourage birds of prey to live and nest within other agricultural habitats.

Relative to vineyards without falcons, the presence of falcons was associated with a lower abundance of non-native focal species and less grape damage associated with non-native and native focal species. All 4 species are part of the diet of New Zealand falcons living in vineyards (Chapter 3). Our findings are likely a result of the combined effects of direct predation and increased predation risk. Direct predation reduces pest bird populations, whereas high predation risk increases antipredator behaviour (e.g., avoidance and vigilance relative to time spent foraging) and may cause birds to forage in suboptimal locations that offer better protection from predators (Lima & Dill 1990; Fernández-Juricic & Tellería 2000; Devereux et al. 2006). In the case of vineyards, this may result in birds foraging more often within shelter at the vineyard edge in order to avoid the more open, and therefore more risky, habitat of the vineyard itself. Or it may cause birds that do venture into the vineyard to forage in locations that are less profitable. In our study, all birds appeared to prefer to feed on grape bunches that were not covered by canopy, but when a falcon was present, blackbirds, song thrushes and starlings appear to have foraged more on grape bunches that were partially covered by canopy. This change in behaviour may limit foraging efficacy and cause a decrease in the number of grapes removed, as observed in this study.

Our findings support previous observations that native silvereyes peck grapes, while blackbirds, song thrushes and starlings remove them (Tracey & Saunders 2003; Saxton et al. 2004). Falcons were not associated with any significant change in silvereye abundance, but they were associated with a significant decrease in the actual damage caused by silvereyes. This paradox is likely a result of the stochastic behaviour and high variance of silvereye abundance (Fig. 2.5d), combined with increased avoidance and vigilance behaviour in the presence of falcons. Further investigation into the behaviour of silvereyes in the presence of a falcon may provide further evidence as to the relationship between the two species.

The elevated damage levels at the vineyard edge are reflective of the habits of silvereyes, song thrushes and blackbirds for foraging near shelter, a behaviour also observed in North American pest birds (Somers and Morris 2002). In concordance with previous findings that starlings prefer to feed in areas further away from bird shelter (Whitehead et al. 1995;

Tracey and Saunders 2003), we observed greater starling abundance in the vineyard interior compared with at the vineyard edge. For individual vineyard managers, in order to use deterrent methods most effectively, it is vital that they be able to identify the areas of their vineyards that are most susceptible to bird damage (Somers and Morris 2002). Starlings descend upon vineyards in large flocks that can sometimes include hundreds of individuals (Somers and Morris 2002). This highly visible flocking behaviour can result in patches of heavy damage within the vineyard interior, which can be difficult for vineyard managers to anticipate, and sometimes results in managers focusing most of their bird deterrent methods on discouraging starling flocks, rather than investing in protecting vineyard edges where most damage is found (Somers and Morris 2002; Tracey and Saunders 2003; this study).

The relation between grape damage levels and the bird-scaring strategies employed by vineyards was not significant. Birds easily become habituated to common deterrent methods, especially if the same methods are used throughout the grape-ripening season (Bomford & Sinclair 2002; Fukuda et al. 2008). Understanding pest bird foraging behaviour may allow better coordination of deterrent methods (Tracey & Saunders 2003). For example, knowing that fewer starlings will forage at the vineyard interior if a falcon is present could encourage more efficient use of deterrent methods at the vineyard edge.

Our sample size was low because of the small numbers of falcons available for introduction into vineyards. Despite this low power, we found significant associations between falcon presence, passerine abundance, and grape damage. We do not think these correlations were spurious because falcons were introduced to these vineyards. In addition, a lower percentage of grapes in the vineyard in which falcons were present in 2009 and absent in 2010 were damaged in 2009, whereas the remaining vineyards showed no significant between-year difference (Fig. 2.6). We believe this finding means the falcon effects are not spurious. Nevertheless, we assumed that the effect of falcon presence was equal within and across the vineyards in which they were present, even though they may not visit all areas of a vineyard with the same frequency, and we did not include the few vines that were covered in bird-exclusion netting in our analyses. Thus, there may be some variation in falcon effectiveness within a given vineyard.

Mitigation of conflicts between humans and wildlife has become a key facet of predator conservation (Treves & Karanth 2003). Agriculture continues to intensify, expand, and infringe

upon areas inhabited by raptors (Perrings et al. 2006), and conservation efforts are threatened when raptors hunt for valuable domestic or game species, and are sometimes killed by humans (Thirgood & Redpath 2008). Our results suggest that threatened falcons can reduce both the number of pest birds and the amount of damage that pest birds cause to wine grapes and that in this instance the goals of agriculture and predator conservation can converge.

ACKNOWLEDGEMENTS

I am grateful to my supervisors Ximena Nelson and Jason Tylianakis for helping to plan these experiments and for providing essential feedback and comments on the analysis and writing of this chapter. E. Fleishman, R. Knight, M. McCarthy, and 2 anonymous reviewers provided helpful comments on the drafts of the manuscript that went on for publication. N. Fox, C. Wynn, and V. Saxton gave advice on methodology. B. Halkett assisted with data collection. Pernod Ricard New Zealand, Marisco Vineyards, Winegrowers of Ara, Cloudy Bay Vineyards, Johnson Estate Vineyard, Stembridge Vineyards, Kersely Vineyards, Redwood Pass Vineyards, Yealands Estate, Koura Bay Estate Wines, and Dumgree Estate provided access and vineyard information.

CHAPTER THREE

A PORTABLE LOW-COST REMOTE VIDEOGRAPHY SYSTEM FOR MONITORING WILDLIFE

Adult female falcon attacks the author in defence of the nest. (Photo: S. Kross)

Kross, S.M. & X.J. Nelson. 2011. A portable, low-cost remote videography system for monitoring wildlife. *Methods in Ecology and Evolution*. 2: 191-196. doi: 10.1111/j.2041-210X.2010.00064.x

ABSTRACT

Remote videography allows continuous and reviewable recording of unique behaviours with minimal disturbance to focus individuals. It is therefore an excellent, although often unaffordable, method for observing the behaviour of wildlife in the field. Here we describe a digital video-based remote videography design that costs under US $900 and requires relatively minimal maintenance. The system is portable and can record continuously or when motion is detected. Using the threatened New Zealand falcon as a model, in a single season of camera deployment we were able to record a number of unique events, including a new prey species for the falcon and the complete depredation of one nest. Only 12% of potential recording hours were lost, the majority of which were as a result of battery failure (45% of failures) or the camera becoming dislodged (34% of failures). This system will be useful for researchers in all fields who require a reliable, cost-effective means of recording wildlife behaviour in remote locations.

INTRODUCTION

As attested by numerous natural history documentaries, well- placed video cameras may permit observation of wildlife behaviour that is unattainable using traditional hide-and- observe methods; a benefit which is of particular importance when the animal in question is poorly understood or rare. Remote videography has applications in any study where behaviour is relevant, and has been used to study a wide assortment of animals, including mammals (e.g. Maniscalco et al. 2006; Bloomquist & Nielsen 2009), reptiles (e.g. Hunt & Ogden 1991), insects (e.g. Stephanou et al. 2000) and even lobsters (*Homarus americanus*; Jury et al. 2001), but has principally been deployed at bird nests. In bird studies, video cameras are normally placed in or near the nests of focal individuals, providing an accurate record of both nestling (M^{c}Donald et al. 2005; Grivas et al. 2009) and parental behaviours (M^{c}Donald et al. 2005; Pierce & Pobprasert 2007). Owing to the nature of video, events can be reviewed repeatedly to gather detailed behavioural information. For example, close inspection of feeding bouts can provide information on food type, biomass and the timing of feeding events (Cutler & Swann 1999; Lewis et al. 2004; M^{c}Donald et al. 2005; Reif & Tornberg 2006). Remote videography also allows for positive identification of nest predators (Leimgruber et al. 1994; Brown et al. 1998; Cutler & Swann 1999; Pietz & Granfors 2000) and can identify nonpredation events that might play a role in nest failure, such as potential predators visiting a nest but not predating eggs (Pierce & Pobprasert 2007), or the effect of human disturbances, such as chainsaw noise (Delaney et al. 1998).

Setbacks of remote videography include the potential impact of camera presence, human scent and human activity on the behaviours of the study species and any prey or predators nearby (Cutler & Swann 1999; M^{c}Donald et al. 2007). The majority of studies investigating the effect of cameras on predation rates have found that cameras have no effect (Leimgruber et al.1994; Sanders & Maloney 2002; Pierce & Pobprasert 2007), or that the presence of cameras decreases predation rates, possibly because predators are wary of the presence of a camera (Herranz et al. 2002; Richardson et al. 2009). However, camera placement can lead to increased nest abandonment (Pietz & Granfors 2000). Additionally, some systems are bulky and difficult to transport, whereas others require frequent visits to change batteries and download video.

A major drawback of remote videography is the prohibitively high cost of video systems leading to limited sample sizes (Brown et al. 1998; Lewis et al. 2004; Pierce & Pobprasert 2007). As video technology becomes more affordable, it is becoming possible for researchers to construct tailor-made camera setups that are as effective and often cheaper than commercial systems (King et al. 2001). We have developed a portable camera system modified from an original design used by the New Zealand Department of Conservation that is able to withstand harsh weather conditions, records and stores digital files, and can be left in remote locations for several days before changing the batteries. The design on which our model was based has been used to monitor and study some of New Zealand's rare birds, such as kokako (*Callaeas cinerea wilsoni*; Innes et al. 1996) and black stilt (*Himantopus novaezelandiae*; Sanders & Maloney 2002).

Our study species, the New Zealand falcon (*Falco novaeseelandiae*; hereafter falcon), has been the subject of relatively little scientific research, despite its threatened status (Miskelly et al. 2008). New Zealand falcons nest in scrapes on the ground in remote and often mountainous regions and are highly aggressive towards intruders near their nest, often repeatedly striking them in the course of nest defence. Because of this, remote videography is an ideal method for studying the nesting behaviour of this species, and is well suited to study any animal that is territorial, highly susceptible to disturbance or is found in inaccessible locations. This camera system was designed with the aim to monitor the nesting behaviour and attendance of breeding falcons, the behaviour of falcon nestlings, the timing of feeding events and the prey species delivered to the nest. As the beginning of a long-term study, we dispatched four separate camera systems to monitor five nests over the 2008/2009 breeding season.

METHODS

Although many early remote videography studies have revealed previously unknown trends at bird nests (see Cutler & Swann 1999), cassette-based systems have limited storage and therefore require up to twice-daily trips to the site to change tapes, or require the use of time-lapse recording which significantly reduces the number of frames in which prey items or predators are visible for identification (Booms & Fuller 2003; Smithers et al. 2003). The recent integration of digital storage capabilities into video monitoring has allowed researchers to make

the switch from videocassette-based systems to digital storage.

Our system uses an SVAT mini portable digital video recorder (DVR, Model CVP800; SVAT Electronics USA, Niagara Falls, NY, USA). The DVR is small (<100 g), and records onto secure digital high capacity cards (SDHC) with a capacity of up to 32 GB, although 16 GB cards (A-DATA Turbo Class 6; A-DATA Technology Co., Taiwan) were used for this study. One potential drawback of digital video is large file size that can quickly fill up a device's room for storage. This system avoids this by automatically compressing all files using MPEG4-SP video and stores them in either NTSC or PAL video format as advanced systems format. At this compression rate, 10 s of daytime footage was stored in 1.2 MB, whereas nighttime footage required only 1.1 MB. At the former rate, the system will record 2.37 h of continuous footage for every 1 GB of storage, regardless of SDHC card size.

To preserve disc space and avoid erroneous recordings, we used only motion detection recording at the falcon nests, but the DVR does have an option for scheduling certain hours of continuous recording throughout the day. The motion detection function works by detecting changes in colour and shape within a selected motion detection area on a 22 x 15 square grid that is superimposed over the camera image. The intensity of motion required to trigger the start of recording is measured by an image variation 'energy' threshold between 1% and 100% and can be set by the user. We set the motion detection threshold between 10% and 15%, and included the entire range of sight of the camera as our motion detection window to start recording as soon as an adult falcon entered the nest. We set video recording to 30 frames per second at 352 x 240 lines, but the DVR can record at lower frame rates and resolution to reduce file size and the camera is capable of recording at a maximum of 420 lines of resolution. All files were recorded with a time and date stamp. While we did not use audio recording, a microphone could easily be attached to the system and the DVR is capable of recording a single audio channel within the same file as the video at a sampling rate of 44.1 KHz (increasing file size by 13%).

The DVR was housed in a waterproof Pelican™ case (Model 1150; Pelican™ Products, Inc., Torrance, CA, USA) equipped with an automatic pressure equalization valve, and modified to include two waterproof Amphenol™ plug connections (series C16-1; Amphenol Corporation, Wallingford, CT, USA) for power and video input and output (Fig. 3.1). We used Amphenol™ plugs for all waterproof connections. To power the system, 12-Volt, 33 Ah deep-

cycle gel batteries (Century Yuasa Batteries Pty Ltd, Carole Park, Queensland, Australia) were used because they do not leak potentially dangerous corrosive electrolytes during transportation, as wet-cell lead acid (car batteries) sometimes do (Reif & Tornberg 2006). The 12 V power from the battery was connected through the Pelican™ case to run along a two-pair shielded communication cable (25 m long x 32 mm wide) and to power the cameras within the nests (Fig. 3.1). This cable also relayed video from the cameras into the DVR. The DVR requires 4.5 V of power, so a fuse-protected DC–DC converter was included within the case. Batteries were connected to a 10-W monocrystalline solar panel (DSE NZ Ltd, Auckland, New Zealand) coupled with an automatic solar charge converter (Projecta SC005; Brown &Watson International Pty. Ltd, Knoxfield, Victoria, Australia) to keep the panel from overcharging or draining the battery.

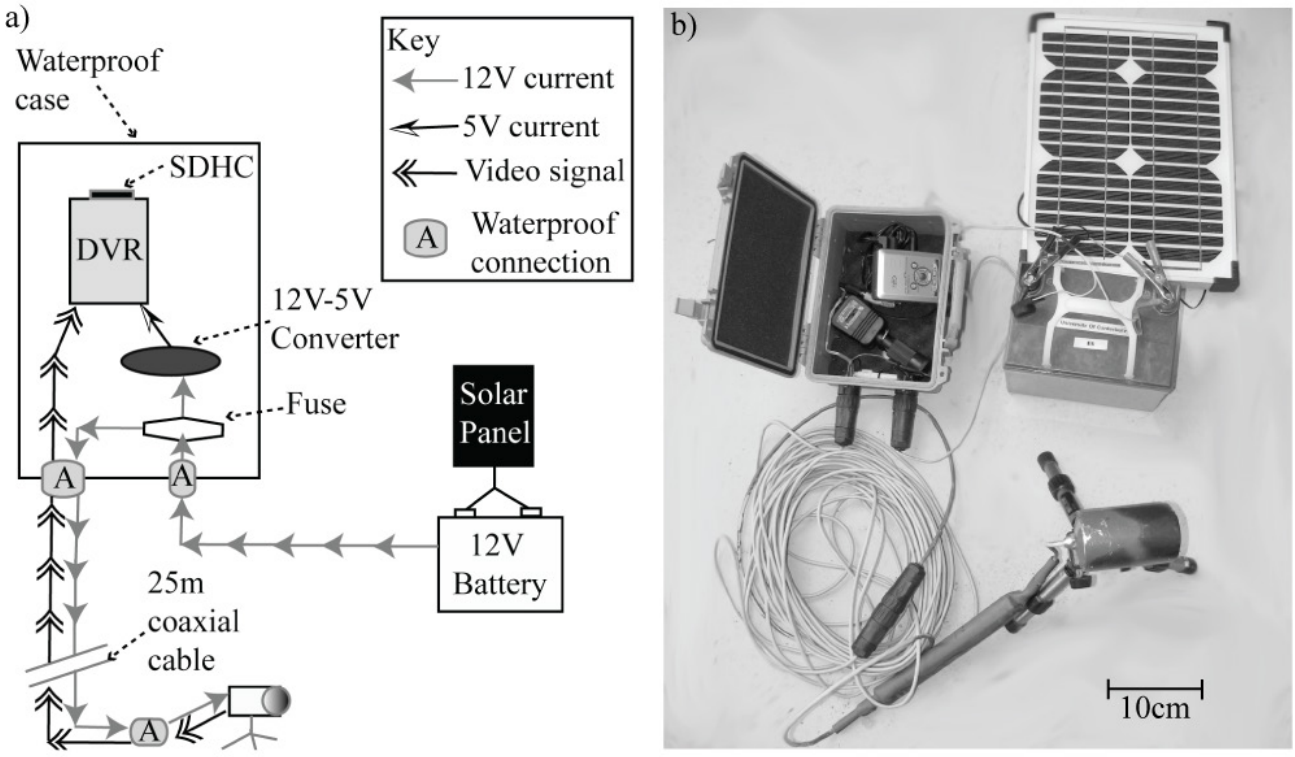

Figure 3.1. (a) Schematic of our remote videography set up. Arrows indicate direction of power and video flow. Note, waterproof connections using Amphenol™ plugs. (b) Photograph of nest camera set up showing (clockwise starting in upper right corner) the solar panel, deep-cycle battery, waterproof video camera on tripod, 25 m of coaxial cable and waterproof case (open) containing digital video recorder (DVR).

We used waterproof (IP68), colour cameras (Swann Security BulldogCam™ CCD) in

NTSC video format with a 1/3" charge-coupled device (Sony Corporation, Tokyo, Japan) with 420 lines of resolution. The cameras have automatic white balance, gain control and backlight compensation. Cameras had a focal length of 6 mm and at a distance of 1 m from the nest had a field of view of *c.* 40º. The camera's minimum focus distance is *c.* 7 cm. Cameras were equipped with 12 near-infrared light-emitting diodes (LEDs) and were able to record black-and-white video at night with a minimum of 0.8 Lux available. The light emitted from these diodes (at a wavelength of 850 nm) is not known to be visible to mammals or birds and previous studies have shown that their use does not affect nesting behaviour or predation rates (Delaney et al. 1998; Pierce & Pobprasert 2007), including among ground-nesting birds in New Zealand (Sanders & Maloney 2002).

To view the menu options, or the image being recorded, the DVR must be connected to a portable screen capable of accepting an RCA connector. We used a portable DVD player (Model DVP-FX720; Sony Corporation) and attached it to the system only when the camera was being set up or when the SDHC card was changed. Consequently, a single portable DVD player was used for all cameras, cutting the cost of maintaining a separate viewer for each camera system.

Fieldwork was carried out in Marlborough, at the Northeast corner of New Zealand's South Island, in the vineyards and surrounding mountains of the Wairau (41.52ºS, 173.872ºE), Waihopai (41.66ºS, 173.575ºE) and Awatere (41.64ºS, 174.073ºE) valleys. The region is mainly arid, with mean rainfall during the October–February falcon breeding season ranging from 45.4 to 71.6 mm and often with extreme temperatures, reaching lows below -1.3ºC and highs above 34.3ºC (NIWA 2010). Falcon nests in the mountains were located in narrow, steep-sided valleys, dominated by a mix of native and introduced grasses, and dense scrub consisting mainly of matagouri (*Discaria toumatou*), bracken fern (*Pteridium aquilinum*) and manuka (*Leptospermum scoparium),* while stands of red beech (*Nothofagus fusca*), silver beech (*Nothofagus menziesii*) and kanuka (*Kunzea ericoides*) were found on valley floors (Fox 1977; Brennan et al. 1993). Falcon nests were also located on steep faces in recently felled *Pinus radiata* plantations that were within 100m of a patch of native forest and also shared similar habitat to the valleys described above. Nests were only accessible by foot and access often required crossing streams, scaling rock faces and breaking through dense vegetation.

Falcons in our study either nested in the hill habitat described above (hill nests), or were

falcons that had been released as part of a reintroduction programme, called 'Falcons for Grapes' (FFG), in the vineyards of Marlborough (vineyard nests). Falcons nesting in vineyard habitat nested initially on the ground and the remote videography system at these nests was set up in the same way as at wild falcon nests (Fig. 3.2c). When the eggs in vineyard nests hatched, FFG often placed the nests into artificial nest barrels that were raised from of the ground. I mounted cameras to the sides of these barrels so that they pointed toward the artificial nest scrape and included a view of the opening at the face of the barrel from which parents entered (Fig. 3.2b and 3.2d).

The entire remote videography set up weighed *c.* 15 kg and fitted easily into a 50L backpack. This system can be set up by only one person, but we always worked in teams of two to ensure the fastest possible system deployment, as our study species was easily disturbed and highly aggressive towards people. One person secured the camera in a location that provided a clear view of the chicks but did not interfere with the falcons entering and leaving the nest, or with regular nest activities (Fig. 3.2a). Meanwhile, the second person ran communication cable to a location where the setup would be stable and hidden from view by vegetation, *c.* 25 m from the nest, assembled the recording station and attached the viewer. At this point, the person remaining at the nest could be instructed as to the best camera angle and whether vegetation in front of the camera needed to be moved or trimmed. Once this was completed, we immediately left the nest area. To determine the impact of our presence at nests, we recorded the time required for camera set up as the time from the onset of nest defence behaviour until the time at which parents stopped defending the nest. All research was performed according to New Zealand Animal Welfare Act 1999 and the University of Canterbury Code of Ethical Conduct for the Use of Animals (University of Canterbury Animal Ethics Committee 2008/ 27R), and under the permission of the Department of Conservation (NM23677 – FAU).

Each camera was checked every 3–4 days, at which point the battery and SDHC card were changed. We always attached the viewer to ensure the camera was still operating and to determine whether the camera had become dislodged, so any problems could be remedied immediately. Video from the SDHC card was copied onto an external hard drive (Maxtor OneTouch 500GB; Seagate Technology, Scotts Valley CA, USA) archived by date. Files were watched individually using Quick- Time Player (version 7.6.4; Apple Inc, Cupertino, CA, USA), permitting inspection from four times normal speed to frame-by-frame analysis. Files

were backed up by burning them onto 4.7 GB writable DVD's (SRO8109; Transonic Industries Ltd, Hong Kong, China).

Figure 3.2. Pictures of remote videography systems at the nests of New Zealand falcons. (a) Volunteer Paul Lintott places a nest camera at a wild falcon nest located on a cliff ledge. (b) Volunteers Paul Lintott and James Crowe suspend a nest barrel mounted with a remote videography system from a tree in a vineyard. (c) A remote videography system on a nest scrape containing four eggs beneath the roots of a fallen tree. (d) Three chicks from the same nest as (c) after being placed in a nest barrel by FFG, camera is visible in upper right corner. (e) remote videography system at a wild falcon nest containing two 1-day-old chicks and an unhatched egg, located under a fallen ponga fern (*Cyathea* spp.).

RESULTS

The components for the recording system were purchased and assembled for a cost of $862 USD per system (Table 3.1), a considerably lower cost than that of most commercially available wildlife surveillance systems. The system draws 3.21 W of power during daytime recording and 3.73 W of power when the LEDs are operating at night. We did not insulate our batteries, and

fluctuations in temperature, especially cold-evening weather, could have lessened their efficiency.

Table 3.1. Price of components for each remote videography system (USD)

Component	Cost per camera (USD)
Waterproof, colour camera	114
Waterproof Pelican™ case	60
Deep-cycle gel battery	94
Solar panel	106
Solar charge regulator	41
DVR	199
16 GB SDHC card	51
Amphenol™ plugs	114
Coaxial cable (25 m)	36
Circuitry (including fuse protector and labour)	47
Total	862

Prices are converted from New Zealand Dollars (conversion date: 5 April 2010) and are rounded to the nearest dollar. Prices do not include shipping costs. Additional components used between all systems included a portable DVD player for field viewing, a battery charger, a portable hard drive, SDHC cards, spare batteries and tripods or other camera-mounting materials. DVR, digital video recorder; SDHC, secure digital high capacity cards.

Five nests were monitored in the first season of camera deployment, four were monitored in the second season (one failed in the incubation stage), and two were monitored in the final season. Cameras were present for a total of 7,117 h at the ten nests, during which time motion could have set off recording. We were interested in recording all falcon movements within the nest. A total of 884.95 h of recording time (12.43% of total deployment time) was lost due to battery failure, mechanical problems, or camera displacement. This is lower than other systems, with published ranges from 11% to 39% (Sabine et al. 2005; Grivas et al. 2009). Battery failure caused a loss of 395.9 h of filming which was 5.56% of the total deployment time. Of all camera failures, 44.74% were because of battery problems. Camera displacement (by the falcons, wild animals, livestock and humans) accounted for 33.83% of failures and the other 21.44% were presumed to be mechanical problems. Fewer than half of the 6,232 hours that were recorded and scored were included in my analysis of breeding behaviour (Chapter 5) because all days that were missing >50% of possible recording hours were removed from the analysis, as were all days after chick age 30d. At nests located on the ground (those not lifted

into barrels by FFG), once the chicks reached 20d old they sometimes left the nest scrape for periods of time, and although this time is included as potential recording hours here, these periods were considered to be without data and caused some days to be removed from analyses.

Using a subset of the 5 nests recorded in 2009, cameras took an average of 11 min 48 s ± 49.2 s (± S.E.M., N = 5) to set up from the time the falcons first started nest defence to the time the assembly was completed and the falcons stopped nest defence. At three of the nests, cameras were placed directly on the ground, at a distance of *c.* 0.5 m from the scrape. At the remaining two nests, falcons had been moved into 'barrels' that were raised off the ground to protect the nest from predators. At these two nests, the cameras were first placed on posts *c.* 1 m from the barrel, and then attached directly to the barrel entrance at a distance of 0.25 m from the nest interior. In two instances, one 'barrel' nest and one ground nest, the falcons returned to incubate eggs or brood chicks less than a minute after we left the nest and in another two, the falcons returned in under 3 min. At one ground nest, it took 65 min for the falcons to return to the nest. Only in the case of the fifth nest did the falcons appear to be disturbed by the camera, often examining it upon entering the nest for the first 3 days following camera placement, but they continued to care for and eventually fledge the chick in this nest. On a few occasions in each nest, the adult falcon appeared to catch its own reflection in the glass covering the camera lens. In these cases, the falcon would approach the camera to examine it and sometimes even try to pick it up, but in every case the falcon returned to normal activities within a few minutes. Using the 10–15% motion detection threshold, 21–49% of our recordings were triggered by the movements of vegetation and invertebrates. One of our primary interests was observing the delivery and handling of prey items (n = 638 events for the first 5 nests). For this, we were able to record video that gave us clear views of at least one defining part of each prey item for 94.8% of the feeding events. The small fraction of feeding events unable to be classified were due to a falcon obscuring the camera's view (2.1%) or because of poor contrast (3.1%). On 4 of the 10 battery-induced failures the occurred in the first season, footage stopped late in the evening and then restarted again the following day, owing to the solar panel recharging the battery to a point where it could run the system – this resulted in an additional 8 days of footage being recorded that would have otherwise been lost.

A negligible number of files (<50 of *c.* 100 000) were lost as a result of file corruption. As is the case with any raw data, backup of files and storage in multiple locations is a necessary

precaution. Depending on the amount of activity in a nest, between 1 and 4 days worth of video could be backed up on a single DVD, however, DVDs were only used as temporary backup as they are known to degrade over time and should not be used for permanent storage of data. External hard drives are a more reliable medium with which to store data long term. This technology has already shown considerable promise, as it has permitted us to observe not only everyday behavioural processes within falcon nests (Fig. 3.3a and 3.3b; Videos 1 and 2), but also numerous behavioural events that would have otherwise been unknown or difficult to substantiate (Video 3 and 4). For example, we recorded a non-predation event in which a young brushtail possum (*Trichosurus vulpecula*) entered the nest at night and was chased away by the female falcon. We also recorded the complete depredation of the nest by a feral cat (*Felis catus*) which was recorded on 15 December (we presumed it killed one chick that night based in the chick's absence in subsequent footage) and then on 17 December (the cat was recognizable by a notch in its right ear), when it killed the remaining two chicks over a period of 10 h (Fig. 2.3c; Video 3; Chapter 7). Finally, we obtained footage of an adult falcon feeding its young with a common gecko (*Hoplodactylus maculatus*), a previously unknown prey item for this species (Fig. 3.3d; Video 4).

Fig. 3.3. Still images taken from video footage at New Zealand falcon nests over the 2008–2009 breeding season in Marlborough, New Zealand. (a) Female falcon feeding her chicks, (b) three chicks fight over a field mouse brought into the nest by the male parent, (c) Feral cat hissing at parents (not in frame) after killing all three 28-day-old nestlings (Video 4, Supporting information), and (d) a common gecko (Hoplodactylus macutus), a new prey item for this species, being offered to a nestling (Video 3, Supporting information).

DISCUSSION

Our system is ideal for monitoring wildlife in most field conditions and, in addition to permitting observation in inaccessible areas (such as the interior of a falcon nest), is capable of recording behaviours in detail and over periods of time that would be unobtainable using

traditional observation methods. The camera system can be easily transported and maintained in the field, and construction of the camera system can be tailored to fit the needs of the researcher: for example, a video camera fitted with a macro lens could be substituted if the researcher were interested in examining invertebrate behaviour. Importantly, the cost of US $850 is low compared with most commercially available systems. This has significant flow-on effects, such as the ability to increase sampling numbers and the concomitant increase in reliable information on the behaviour of animals in natural habitats. Indeed, video has been shown to be a more accurate method of assessing raptor diet than indirect methods, such as analysing prey remains and castings (Lewis et al. 2004; Reif & Tornberg 2006), and because field observers often suffer from fatigue, video is considered more accurate than direct observation from hides (Delaney et al. 1998).

An important aspect of our design is the ability to leave the camera in the field for 4 days at a time between maintenance visits. Compared with other remote videography systems that require more frequent visits, sometimes multiple times a day, this significantly lowers the impact that human presence may have on the focal animals, as well as drastically reducing the number of human hours needed for this aspect of the research. In the case of easily disturbed or aggressive animals, such as our study species, it is of particular benefit to use a system that requires infrequent maintenance visits.

One concern we had was the length of time that it took for the falcons to return to the fifth nest. This may have been due to the chick's age and its parents' previous experience. Unlike all other nests sampled, a chick had been removed from this nest only 2 days prior to camera placement as part of a local conservation project. Additionally, when the camera was placed in the four other nests, the falcons were either incubating eggs or brooding chicks <5 days old, whereas at the fifth nest the parents were caring for a single chick that was *c.* 12 days old, an age at which chicks have begun to thermoregulate and no longer need constant brooding (Fox 1977). Importantly, none of the nests were abandoned because of the presence of the camera; however, it is important to note that the presence of cameras may have both obvious and discrete disturbance effects on the behaviours of the study species in question (M^{c}Donald et al. 2007). In our case, cameras were all located <1 m from the nest, and falcons appeared to accept them. Nevertheless, we have noted all interactions with the camera for use in our future analysis of falcon behaviour. Because cameras were not visible from outside the nest, it seems

very unlikely that the cat that depredated one of the nests perceived the camera within and was attracted to it. Furthermore, even within the nest, the footage clearly showed that the cat ignored the camera, suggesting it did not play a role in nest predation.

Video is engaging, entertaining, and can generate interest and empathy for the subject. Because digital video can be easily disseminated through outlets, such as popular media and the Internet to reach a wide audience, it can be used as an educational tool to promote conservation. For example, our video of normal falcon behaviour within nests and of depredation of falcon chicks by the feral cat has already been used in schools to encourage falcon conservation and better predator control, as well as being aired on New Zealand national television.

As an affordable and customizable remote videography system, our design can be implemented across a variety of taxa and in a range of field conditions at adequate sample sizes. Video is a desirable means of collecting behavioural information in animals ranging from invertebrates in the field to wild birds, livestock and companion animals (Wratten 1994). This system is ideal for researchers in any field needing to obtain detailed information on the behaviour of rare or inaccessible species with minimal disturbance to the focal individuals. Continued use of remote videography in the field of wildlife management will inevitably lead to further discoveries of new behaviour, while the ease of dissemination of digital video will aid in conservation initiatives and education.

ACKNOWLEDGEMENTS

I am grateful to my supervisor, Ximena Nelson, for valuable advice on camera design and use, and for providing essential feedback and comments on the writing of this chapter. We are grateful to Pernod Ricard NZ and C. Monk for electrical work on systems and to H. Oliver and all other volunteers who helped with camera set up and maintenance. We are also grateful to the landowners who gave access to the falcon nests. N.C. Fox and C. Wynn provided advice on falcon nesting biology and assisted in locating nests, whereas A.Woods provided electrical advice. Three anonymous reviewers, S. Cockburn and P. Gaze of DoC provided helpful advice on this manuscript, and the latter two also gave invaluable advice on the design of the remote videography system and on DoC's previous use of their system.

SUPPORTING INFORMATION

A DVD has been included with this thesis containing clips of footage from the falcon nests. The first four clips on the DVD are relevant to this paper:

- Video 1. Video clip showing both adult New Zealand falcons at a nest during the incubation period.
- Video 2. Videos showing New Zealand falcons feeding their nestlings.
- Video 3. Video clip showing female New Zealand falcon feeding a common gecko (*Hoplodactylus maculatus*), a new prey item for the falcon, to a nestling.
- Video 4. Video of a feral cat killing two 28-day old New Zealand falcon nestlings. Video has been edited from a two-hour event. All three nestlings from this nest were killed by the same feral cat.

CHAPTER FOUR

DIET COMPOSITION AND PREY CHOICE OF NEW ZEALAND FALCONS NESTING IN ANTHROPOGENIC AND NATURAL HABITATS

Adult male New Zealand falcon with a freshly-caught juvenile goldfinch (Photo: S. Kross).

Kross, S.M., Tylianakis, J.T. & X.J. Nelson. In Press. Diet composition and prey choice of New Zealand falcons nesting in anthropogenic and natural habitats. *New Zeland Journal of Ecology.*

ABSTRACT

As part of a study to assess the value of vineyards as habitat for the threatened New Zealand falcon (*Falco novaeseelandiae*), we used remote videography and prey remains to examine the diet composition of four pairs of nesting falcons that had been relocated into a vineyard-dominated landscape, and compare it with that of six pairs nesting in their natural habitat in nearby hills. We also quantified the abundance and species composition of avian prey in the habitats surrounding each falcon nest. The composition of available prey did not differ between the two habitats, nor did the composition of avian species in the diet of falcons. Avian prey was the main food source for falcons, representing 97.86% of prey items by frequency and 83.28% of prey items by biomass. Mammals represented only 1.86% of prey items by frequency, but made up 16.69% of prey items by biomass. We also found that falcons preyed upon introduced species more than would be expected, and on endemic species less than would be expected, based on their availability in the landscape. The absence of any significant diet differences between native and vineyard habitats suggests that the latter may be a viable alternative when natural habitats are unavailable.

INTRODUCTION

Agricultural primary production systems occupy over 35% of the ice-free land area of the world (Foley et al. 2007) and almost 60% of New Zealand (MacLeod et al. 2008). This prevalence, and the global decline in natural areas mean that production systems are increasingly being viewed as areas in which biodiversity conservation should be carried out, in addition to conservation reserves (Edwards & Abivardi 1998; MacLeod et al. 2008). Reintroductions of extirpated species are one way in which primary production systems can increase local biodiversity. However, for reintroduction projects to be successful, the targeted area for release must contain the habitat and food resources needed to support natural behaviour and survival of the reintroduced individuals (Armstrong & Seddon 2007). Additionally, the threats that caused the decline of the target species in the region in the first place must be removed (Fisher & Lindenmayer 2000; Armstrong & Seddon 2007).

A recent project in New Zealand has focussed on the reintroduction of the country's only remaining endemic bird of prey, the threatened New Zealand falcon, (*Falco novaeseelandiae*; Miskelly et al. 2008), into the country's largest wine-growing region, Marlborough (MAF 2009a). The idea hinges on the notion that reintroduced falcons will have increased access to their primary prey: passerine birds (Fox 1977; Barea et al. 1998; Seaton et al. 2008), because vineyards represent an abundant food source for passerines in the autumn and winter (MAF 2009a). Indirect evidence suggests that this may be true. Falcons in vineyards have higher nest attendance, higher brooding rates, and higher feeding rates, and have also been found to feed their chicks larger prey items and a greater total biomass of prey compared with falcons in the hills (Chapter 5). However, studies of raptors overseas have sometimes shown that vineyards are poor foraging habitat for some birds of prey (e.g. Swolgaard et al. 2008), and therefore it is important to determine if the vineyard environment may be changing the foraging habits of translocated falcons.

Previous studies on the diet of *F. novaeseelandiae* have focused on collections of prey remains and regurgitated pellets of undigested material (Fox 1977; Seaton et al. 2008), even though these methods are known to be biased (Redpath et al. 2001; Tornburg & Reif 2007). In one exception, Barea et al. (1998), used remote videography to study the diet of two pairs of

nesting New Zealand falcons in a forested area on the North Island. In studies of overseas raptors, remote videography has been shown to be more accurate than the aforementioned indirect methods (Gronnesby & Nygard 2000; Lewis et al. 2004; Reif & Tornberg 2006), and more accurate than direct observations from hides (Delaney et al. 1998; Rogers et al. 2003). Remote videography also has the additional benefits of recording behaviours associated with prey handling, juvenile development and of obtaining recordings of potential predators at nest sites (Delaney et al. 1998; Cutler & Swann 1999; Lewis et al. 2004; M^{c}Donald et al. 2005; Chapter 3).

Our study provides essential information on the impact of habitat change on the diet of New Zealand falcons living within vineyards. We use remote videography as well as analysis of prey remains to assess the diet composition of falcons nesting in vineyards and of falcons nesting in the hills. We also compare these diet compositions with the availability of avian prey in the surrounding landscapes to determine if falcons are selecting for or against specific prey species, and whether differences in prey availability in vineyards vs. hills leads to differences in prey selection.

METHODS

Study area

Our study was based in the Wairau, Waihopai, and Pelorous valleys of the Marlborough region, and their surrounding hill habitats. We interviewed local farmers and forestry workers in order to locate falcon nests. Six non-vineyard falcon nests ('hill nests') were found either in steep-sided valleys dominated by a mix of native and introduced grasses and dense scrub or in hillside forestry (*Pinus radiata*) plantations (Chapter 3). In contrast, four falcon nests ('vineyard nests') were near the valley floor, usually within a vineyard, although occasionally within forestry plantations adjacent to a vineyard. The key differences were that vineyard adults were provided daily with one-day-old poultry chicks as supplementary food on an *ad hoc* basis (though these were excluded from our analyses), and that falcons nesting in vineyards had their nests raised from the ground in order to reduce the chances of predation by invasive mammals. Vineyard falcons had all been translocated as chicks as part of the reintroduction project, and were at least one year old at the time of nesting.

Prey abundance

Five minute bird count methods (Bibby et al. 2000) were used at four different representative habitat locations within 500 m of each falcon nest site. All birds that were seen or heard within 50 m of the centre of the count location were identified and counted. We took precautions to avoid counting the same individuals more than once in a single count: birds heard singing from the same location, seen after hearing the song of the same species from a similar area, or seen flying to multiple locations during the 5-minute count were only counted once. Count locations were at least 150 m apart. Bird counts were made on at least three separate occasions at each nest site, with data pooled across the representative habitats for each date that counts were conducted. Birds were categorised as either introduced, native, endemic, or unknown. Endemic species are those that are found naturally within New Zealand and breed only within New Zealand. Native species are found naturally within New Zealand, but also breed in other areas of the world. Introduced species are those that did not occur within New Zealand prior to human arrival and that were aided in their colonisation by human activities.

New Zealand pipit (*Anthus novaeseelandiae*) were never observed in our prey abundance counts. New Zealand pipit display different behaviours, but are physically very similar to the introduced skylark (*Alauda arvensis*), so while we could be confident that our prey abundance counts did not include pipits, they may have been included in the diets of falcons. As has been the case in previous studies (Fox 1977; Barea et al. 1998; Seaton et al. 2008), we have pooled the data between these two species and therefore assumed that any prey remains characteristic of the two species actually did belong to skylarks, which were common in both of our study habitats. We also pooled together the introduced cirl bunting (*Emberiza cirlus*) with the yellowhammer (*Emberiza citrinella*) because of the close relatedness of these two species and because deciphering between the two species in prey remains is difficult.

Prey remains

Prey remains were collected opportunistically from nine of the ten nests included in this study, the tenth nest was depredated by a feral cat prior to collection of prey remains and samples could not be taken. Remains were found within the nest scrape and the surrounding 50 m. Prey

remains included any feathers, fur, beaks, feet, or bones that had not been consumed by falcons. Any of these items found within 50m of a falcon nest were considered to have been falcon prey. When samples were collected from nests, all visible feathers and prey remains were removed, so that samples collected on different dates represented new prey items (Fox 1977). Samples were frozen, and then sorted by date and identified through comparison with reference collections at the University of Canterbury and at the Canterbury and Te Papa museums. Diagnostic features were used to determine the minimum number of individuals that could be present in each sample. Based on these analyses, all birds were classified as introduced, native, endemic, or, rarely (0.98%), unknown.

Remote videography

We used a portable remote videography system with a near-infrared camera placed at the edge of the nest or mounted to the side of nest barrels in the case of vineyard nests. The system uses motion-detection and was set to record at 30 f.p.s. (Chapter 3). This recording system has been shown to lose only 16% of potential recording hours, primarily due to battery failure or camera dislodgement (Chapter 3). We recorded for 101 days (1473 recording hours) at the six hill nests and for 88 days (1333 recording hours) at the four vineyard nests.

Video was reviewed using Quick-Time Player (version 7.6.4; Apple Inc, Cupertino, CA, USA) at a maximum speed of four times normal speed to a minimum speed of frame-by-frame, allowing quick review of non-important files and detailed review of important events. All feeding events were examined frame-by-frame to identify prey items to the most specific taxonomic level possible.

Prey that could not be identified to species level were identified to family or order. Avian prey were aged according to feather structure: birds with completely sheathed feathers were considered nestlings, those with partially sheathed feathers were considered fledglings, and those with unsheathed feathers were considered adults (Lewis et al. 2004). The amount of prey handling prior to parents delivering the item to chicks was noted, with prey being either completely plucked (no wing or tail feathers remaining), partially plucked (some wing or tail feathers remaining) or not plucked (all wing and tail feathers intact). We also noted whether or not prey were decapitated.

Statistical analyses

For each species identified, we counted the number of prey items as either the number observed in the video or the number counted from the prey remains, whichever was higher. We compared the abundance of each prey species between vineyard and hill nests (with all nests pooled for each habitat type) using paired and unpaired t-tests and Wilcoxon rank sum tests. We used Chi-square (χ^2) tests of independence to compare the selection of the different categories of avian prey between falcons in the two habitats, as well as to compare abundance of different prey types in the diet of falcons with the abundance of those prey types in the surrounding habitats. We used a generalised linear mixed model in the lme4 package (Bates et al. 2008) R (v 2.7.2; R core development team 2008) to determine if falcons chose prey items based on prey availability or prey biomass. Prey biomass was the mean adult biomass for each species given in Heather & Robertson (2000; Table 4.1). We modelled the relative proportion of each species in the diet of falcons (each prey species being a replicate) with the relative proportion of each species in the surrounding habitat, the endemicity of each species, the habitat type of the nest (vineyard or hill), and the biomass of each species as predictors. Interaction terms were included between all fixed effects in the maximal model. We also included second- and third-order polynomial terms for the biomass of each species in order to account for potential nonlinear response of falcons to prey biomass (e.g., preference of prey over a threshold size). Nest site and prey species were included as crossed random effects to account for the non-independence of prey items in a given nest, and to test for the effects of availability and biomass on attack rates of each species. We simplified models by first removing non-significant interaction terms, then the polynomial terms, and then main effects until no further reduction in residual deviance (measured using Akaike's Information Criterion, AIC) was obtained. We then compared the model estimates for relative proportion of each species in the diet of falcons with the actual observed relative proportions to determine if falcons were taking individual species more or less than would be expected. We used a Markov chain Monte Carlo (MCMC) resampling method with 10,000 simulations to estimate *P* values and high posterior density (HPD) intervals for the fixed effects (carried out using the 'pvals.fnc' function in the

LanguageR package (Baayen 2008) in R). Only individuals positively identified to species level were included in our analysis of falcon prey choice, with all unidentified birds excluded.

RESULTS

Prey abundance

All values are presented as the mean ± 1 S.E.M. There was a non-significant tendency for vineyards to have more total birds counted during 5-minute bird counts compared with hill habitat ($t_{6.38} = 1.62$, $p = 0.15$). In vineyards, a mean of 75.99 ± 9.71 birds were counted per visit, whereas in the hills a mean of 55.97 ± 7.58 birds were counted. Vineyards had a higher abundance of introduced birds than did hill habitat (vineyards, 61.09 ± 8.30; hills, 36.25 ± 3.98; $t_{4.4} = 2.70$, $p = 0.049$), while hills had a higher abundance of native birds than did vineyards ($t_8 = 2.26$, $p = 0.051$; Fig. 4.1). There was no significant difference in the number of endemic birds ($t_8 = 1.16$, $p = 0.28$), or in the number of unidentified birds (W = 5, $p = 0.16$; Fig. 4.1).

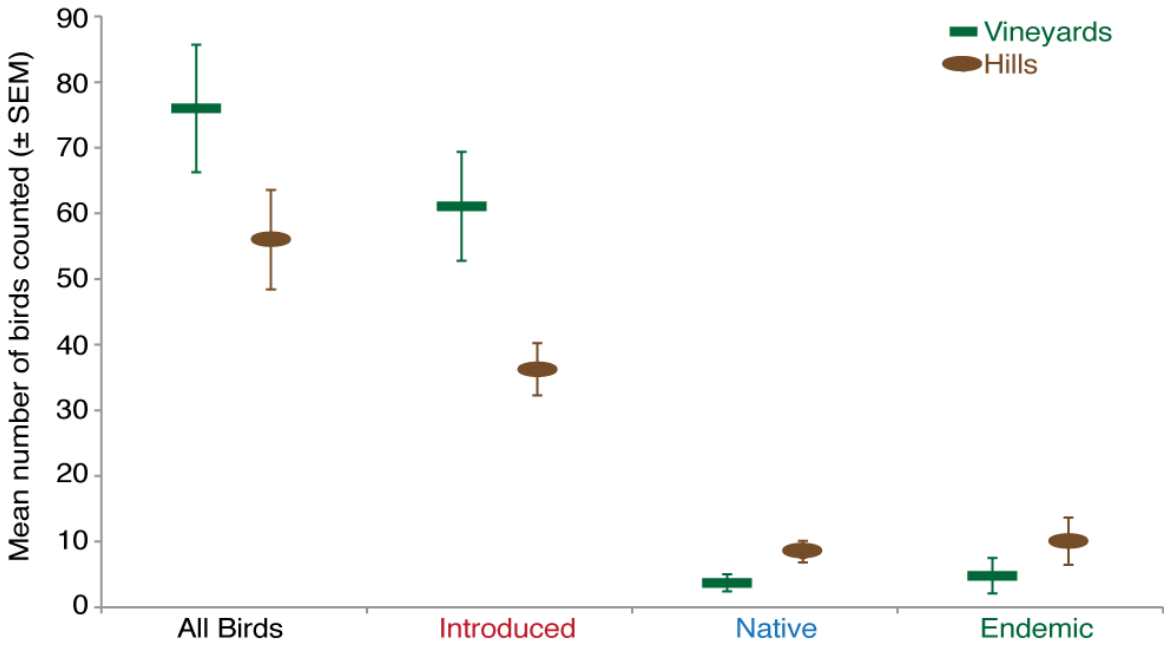

Figure 4.1. Mean (± SEM) abundance of birds counted and of the avian prey of the New Zealand falcon grouped according to endemism in representative habitats near nests in vineyard and hill habitats in Marlborough. The density of introduced birds ($t = 2.70$, $p = 0.049$) and native birds ($t = 2.26$, $p = 0.051$) differed significantly between the two habitats.

Prey identification and characteristics

Falcons primarily fed their chicks avian prey, which by number comprised 97.86% of prey, and by biomass 81.11% of prey (Table 4.1). A total of 2,056 individual avian prey items were identified using a combination of video (n = 1,990) and prey remains (n = 205). We counted an average of 205.6 ± 23.21 avian prey items at each nest using these two techniques together. Of the prey remains found in nests, 66 represented prey that were not identified using video. On average, prey remains alone accounted for 3.83 ± 1.41% of the prey items included in our analysis. Analysis of prey remains significantly underestimated the total number of prey items delivered to the nests compared with that found using remote videography (t_{16} = 46.35, p < 0.001). Prey remains detected an average of 11.53 ± 2.55% of prey items, while remote videography detected an average of 95.45 ± 1.42% of prey items. Overall, 955 avian prey items were identified to the species level. An additional 156 prey items were identified as unknown finches, 11 were identified as unknown Galliformes, and 1,225 were identified as unknown Passeriformes.

Thirty-eight mammalian prey items were recorded using video, with one additional mammalian prey item identified using prey remains. Of these, 30 were recorded at nests in the hills and ten were recorded at nests in the vineyards (Table 4.1). Mammals represented 2.39 ± 0.75% of the prey items delivered to hill nests and 0.88 ± 0.46% of the prey items delivered to vineyard nests, although this difference was not statistically significant ($t_{7.6}$ = 1.72, p = 0.12). In both habitats combined, mammals represented only 1.90% of prey items by frequency, but made up 16.69% of prey items by biomass (Table 4.1). Three arthropod prey items were identified using prey remains, with one of those also identified on video. Three reptiles were identified on video but were not identified using prey remains, with two of these recorded at vineyard nests.

Table 4.1. Prey species delivered to chicks at the nests of four pairs of New Zealand falcons breeding in vineyards and the nests of six pairs of falcons nesting in the hills.

Prey Species	Mass (g)*	% frequency in diet	Percent total biomass
Birds			
Endemic			
Grey Warbler (*Gerygone igata)*	6.5	0.62	0.12

Prey Species	Mass (g)*	% frequency in diet	Percent total biomass
Fantail (*Rhipidura fuliginosa)*	8	0.29	0.07
Bellbird (*Anthornis melanura*)	30	0.19	0.17
Brown Creeper (*Mohoua novaeseelandiae*)	13.5	0.14	0.06
Long tailed cuckoo (*Eudynamys taitensis*)	125	0.05	0.18
Tui (*Prosthemadera novaeseelandiae*)	105	0.05	0.15
Banded Dotterel (*Charadrius bicinctus*)	160	0.05	0.23
Tomtit (*Petroica macrocephala*)	11	0.05	0.02
Weka (*Gallirallus australis*)	850	0.05	1.23
Rifleman (*Acanthisitta chloris*)	7	0.05	0.01
Kereru (*Hemiphaga novaeseelandiae*)	650	0.00	0.00
Native			
Silvereye (*Zosterops lateralis*)	13	3.43	1.35
Introduced			
Greenfinch (*Carduelis chloris*)	28	6.71	5.70
Chaffinch (*Fringilla coelebs*)	22	5.09	3.40
Goldfinch (*Carduelis carduelis*)	16	4.19	2.03
Blackbird (*Turdus merula*)	90	2.19	5.97
Yellowhammer (*Emberiza citrinella*)	27	1.81	1.48
Song Thrush (*Turdus philomelos*)	70	1.09	2.32
Skylark (*Alauda arvensis*)	38	1.09	1.26
House sparrow (*Passer domesticus*)	30	1.05	0.95
California quail (*Callipepla californica*)	180	1.14	6.23
Starling (*Sturnus vulgaris*)	85	0.95	2.45
Dunnock (*Prunella modularis*)	21	0.57	0.36
Redpoll (*Carduelis flammea*)	12	0.48	0.17
Feral pigeon (*Columba livia*)	400	0.05	0.58
Pheasant (*Phasianus colchicus*)	1300	0.10	3.75
Little owl (*Athene noctua*)	180	0.10	0.52
Duck spp.	40	0.05	0.06
Unidentified Finch	20	7.43	4.50
Unidentified Galliform	27.5	0.52	0.44
Unidentified Passerine	20	58.31	35.35
Total endemic birds		1.52	
Total native birds		3.43	
Total introduced birds		26.65	
Total birds		97.86	81.11
Mammals			
European hare (*Lepus europaeus*)	1781	0.14	7.71
Stoat (*Mustela erminea*)	270	0.10	0.78
Rabbit (*Oryctolagus cuniculus*)	607	0.52	9.63
House mouse (*Mus musculus*)	17	0.67	0.34
Rat spp.	25	0.48	0.36
Total mammals		1.90	18.82
Insects			
Huhu beetle (*Prionoplus reticularis*)	2	0.05	0.002
Dragonfly spp.	2	0.05	0.002
Total insects		0.10	0.01
Reptiles			

Prey Species	Mass (g)*	% frequency in diet	Percent total biomass
Skink spp.	10	0.10	0.03
Common gecko (*Hoplodactylus maculata*)	20	0.05	0.03
Total reptiles		0.14	0.06

*Bird mass is the mean adult weight of each species taken from Heather & Robertson (2000). The mass for duck spp. is the mean mass of individuals delivered to falcon nests as part of this study. Mass for mammals was taken as the mean weights of actual prey items taken by New Zealand falcons in our study area as recorded by Fox (1977).

Prey selection

There was no difference between the proportion of introduced birds found in the diet of falcons in hills and vineyards, when compared with the abundance of introduced birds in the respective surrounding habitats ($\chi^2 = 1.31$, $p = 0.25$). There was also no difference between the proportion of native ($\chi^2 = 1.01$, $p = 0.31$) or endemic ($\chi^2 = 0.01$, $p = 0.93$) birds found in the diet of falcons in either nest type, when compared with the abundance of those birds in the surrounding habitats. Similarly, nest site location (vineyard or hill) was removed from our generalised linear mixed model for proportion of prey species in the diet of falcons. For this reason, we pooled data from both nest types when analysing prey selection.

In general, falcons in both habitats selected introduced birds more than would be expected from their abundance in the surrounding habitat (Figure 4.2). Falcons selected introduced species more than they selected native species ($\chi^2 = 5.85$, $p = 0.02$) and more than they selected endemic species ($\chi^2 = 54.02$, $p < 0.0001$). Falcons also selected native species over endemic species ($\chi^2 = 19.60$, $p < 0.0001$).

The results of our generalised linear mixed model, which treated each species as a separate replicate, supported the results of the χ^2 tests of independence. The best-fit model included only the main effect terms for endemicity, prey abundance, and prey biomass. The model predicted that, holding all other variables constant, the proportion of falcon diet consisting of endemic species did not differ significantly from zero (intercept $t = 1.41$, $p_{MCMC} = 0.12$), and that the proportion of falcon diet consisting of introduced species was significantly greater then endemic species ($t = 4.50$, $p_{MCMC} = 0.0001$). There was no significant difference between the proportion of falcon diet consisting of native vs. endemic species ($t = 1.02$, p_{MCMC}

= 0.27). The relative abundance of each species in the surrounding habitat had a very strong influence on the proportion of each species in the falcons' diet ($t = 11.89$, $p_{MCMC} = 0.0001$).

We found that some species were selected more than would be expected from our model estimates, and some were selected less (Fig. 4.2). All endemic species occurred below the fitted relationship between the proportion of each species in the diet of falcons and the relative abundance of those species in the surrounding habitat. Redpoll (*Carduelis flammea*) and goldfinch (*Carduelis carduelis*) also occurred in lower proportions in the falcons' diet than would be expected from their abundance. Greenfinch (*Carduelis chloris*), blackbird (*Turdus merula*), song thrush (*Turdus philomelos*), starling (*Sturnus vulgaris*), and house sparrow (*Passer domesticus*) all occurred in higher proportions in the diet of falcons than would be expected based on their abundance.

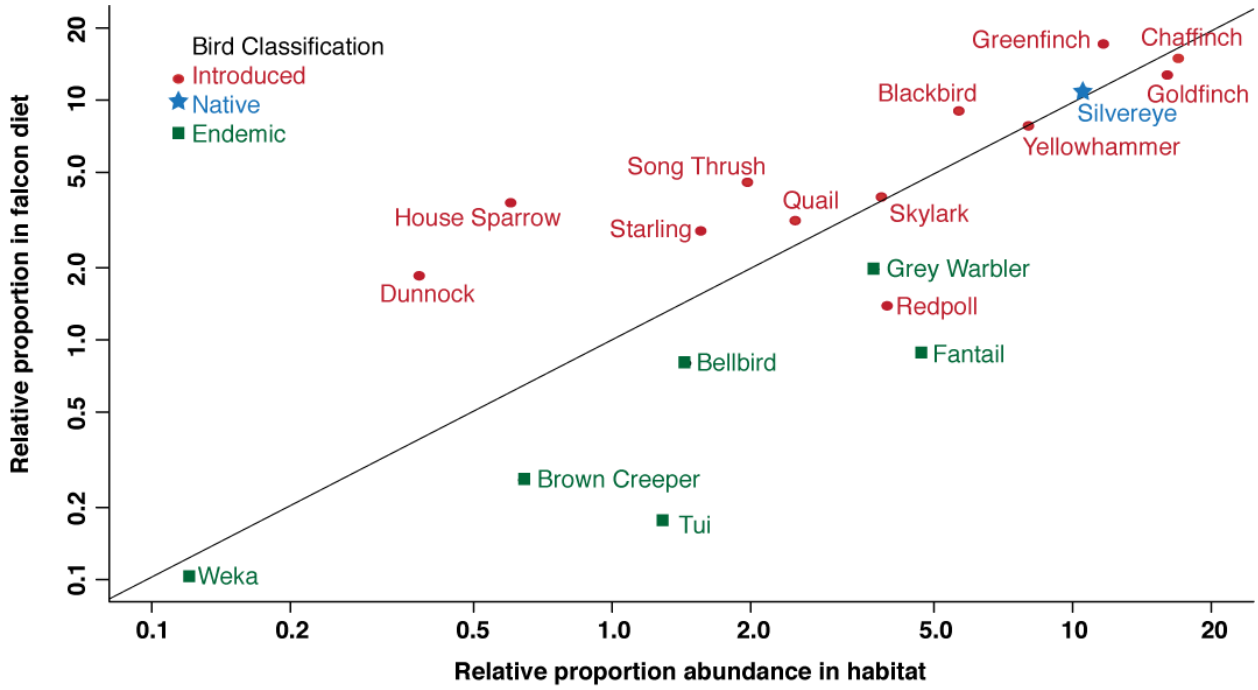

Figure 4.2. Prey selection of New Zealand falcons expressed as a relationship between the proportion relative abundance of each species in the diet of nesting falcons and the proportion relative abundance of each species in the surrounding habitat. The diagonal line represents the fitted slope of the relationship from a generalised linear mixed model, holding bird classification (i.e. endemicity) and biomass constant. Only identified avian species were considered for this analysis. Species have been classified according to endemism to New Zealand. Species not shown were either found at 0% abundance in the habitat (introduced species: feral pigeon, pheasant, little owl, duck spp.; endemic species: long-tailed cuckoo, banded dotterel, tomtit, rifleman), or were found at 0% abundance in the diet (native species: welcome swallow; endemic species: kingfisher, kereru). See Table 4.1 for scientific names.

DISCUSSION

Many previous studies have assumed that predators such as New Zealand falcons are opportunistic, and will choose prey based on their availability in an area (Fox 1977; Barea et al. 1998; Seaton et al 2008). Our results suggest that this is not true, and specifically that falcons are choosing (or are more effective at capturing) introduced avian prey over prey that they evolved hunting. The explanation for this is most likely behavioural or nutritional: endemic birds may have better anti-predator behaviour specific to avoiding falcons, compared with the anti-predator behaviour of introduced birds. Alternatively, endemic birds may not have the same nutritional makeup as introduced birds. Further research into these hypotheses may shed light on this issue.

Falcons appear to select for introduced species and to select against endemic species. Similarly, falcon presence in vineyards has been shown to reduce the abundance of introduced pest birds, but not the abundance of native pest birds (Chapter 2). Our findings are congruent with those of Seaton et al. (2008), who found that many of the endemic species in their study area, a *Pinus radiata* plantation on the North island, were selected against by foraging falcons, while an early observational study by Fitzgerald (1965) on the South island also found that, while endemic species were found in the nearby habitat, falcons were primarily feeding their juveniles with introduced birds. This provides further evidence for the important role that falcons play in natural ecosystem functioning, as it suggests that the presence of a falcon in an area will decrease the introduced avian fauna faster than it will deplete the endemic avian fauna. Importantly, these findings suggest that, despite being an apex predator, the presence of falcons will not deplete the endemic avifauna of an area, particularly of the more common species such as the tui (*Prosthermadera novaeseelandiae*), that are being encouraged to re-colonise Marlborough.

Our study area is characterised by arid hills used primarily for stock grazing and river valleys used for intensive viticulture; both of which are dominated by introduced bird species. Therefore, we do not know what falcon diet preferences would be if introduced birds were not the dominant species in an ecosystem, such as in native forest where endemic species would be relatively much more abundant. However, in a study based on two pairs of falcons nesting in

native forest on the North Island, endemic species were found to contribute a quarter of the birds fed to chicks, and half of the avian prey was introduced species (Barea et al. 1998).

We did not analyse pellets as part of this study. Pellet analysis can provide an indication of how often specific prey species are consumed by birds of prey (Redpath et al. 2001) and can be used to calculate the relative occurrence of prey species in the diet. However, these calculations can be confounded by the number of chicks in a nest, because the same prey item can appear in multiple pellets produced by different chicks. Both pellets and prey remains can be biased because of the amount of prey handling that occurs outside of the nest prior to delivering prey to chicks (Gronnesby & Nygard 2000), and the breakdown of these materials in rainy conditions. In a previous study, pellets contributed approximately 38% of the count of avian prey items for each falcon nest (see appendices in Fox 1977). That study estimated that the number of birds eaten in each nest was 45.37, with a maximum of 91 birds identified at a single nest (Fox 1977). Here we found evidence of an average of 205.6 avian prey items at falcon nests, with a minimum of 93 prey bird individuals counted at one nest (which had a shorter recording period than others) and a maximum of 331 bird prey counted at another. The use of video monitoring also gave insight into the prey handling of falcons, and allowed us to identify that falcons decapitate and/or pluck the feathers from a large number of their prey prior to delivery to the nest (Chapter 5). This may explain why indirect methods such as analysis of prey remains and pellets, even when combined, still considerably underestimate the total number of avian prey consumed.

Previous studies have detected mammals at lower frequencies than we observed in falcon diets, but have still estimated that mammals make up a much larger proportion of the biomass fed to chicks (Fox 1977; Seaton et al. 2008). We found that mammals contributed a small proportion of the diet by both frequency and biomass when compared to previous studies, and this reflects the tendency of indirect methods to overestimate the importance of mammals in the diet of birds of prey.

As has been shown in studies from other parts of the world (e.g., Mersmann et al. 1992; Gronnesby & Nygard 2000; Lewis et al. 2004; Margalida et al. 2005), video was a superior method for the detection of prey items and for the identification of prey, although analysis of prey remains can be less costly and more time efficient than the use of video. Our results suggest that the use of indirect methods is useful for the identification of prey species in the diet

of falcons, but that these methods should not be used to determine the relative importance of species in the diet of falcons or to calculate the total number of prey taken. This study highlights the negative bias that prey remains have for the number of avian prey items and the relative importance of avian prey in the biomass fed to falcon chicks.

Although an increasingly common conservation method, reintroduction projects are financially costly and often do not achieve their goals or do not report on their outcomes (Fisher & Lindenmayer 2000). For reintroduction projects to be successful, relocated individuals must be capable of displaying natural behaviours, and the target release sites must provide relocated individuals with the food and shelter resources needed for survival (Fisher & Lindenmayer 2000; Armstrong & Seddon 2008). Although not statistically significant, the higher density of prey items in vineyards has implications for both adult falcons and their young. Higher prey abundance leads to higher breeding success and lower adult mortality rates (Daan et al. 1996), and is important for raptors residing in agricultural landscapes (Rodríguez et al. 2006). Feeding rates and prey availability, through their effect on nestling development, even have impacts on long-term behavioural characteristics such as foraging (Arnold et al. 2007). We have previously shown that falcons nesting in vineyards have higher nest attendance rates and feed their chicks more than falcons nesting in the hills (Chapter 5), and that falcons living in vineyards provide ecosystem services in the form of reduced pest bird abundance and associated damage to grape crops, with associated economic benefits for viticulture (Chapter 2). Here, we have shown that the diet and prey choice of falcons living in vineyards does not differ significantly from that of their counterparts in the hills. This is important in assessing whether reintroducing falcons into vineyards has a conservation benefit for the species.

ACKNOWLEDGEMENTS

I am grateful to my supervisors Ximena Nelson and Jason Tylianakis for helping to plan these experiments and for providing essential feedback and comments on the analysis and writing of this chapter. For advice, assistance with locating nests and placing cameras we thank: C. Wynn, N. Fox, H. Oliver, L. Olley, P. Lintott, J. Cooper, J. Crowe, B. Coles, J. Knott, J. Kumagai, K. Morgan, X. Birch, R. Seaton, D. Harliwich and E. Soper. For access to land, we thank: Nelson Forests Ltd (D. Parsons), Winegrowers of ARA, Nelson Forests Ltd, Marisco Vineyards (R.

Clare), M. Gifford, Spray Point Station (J & R Mapp), Richmond Brook Station, Wye Hills Farm (E & J Rentoul), as well as all landowners who provided access for falcon nest searches. E. Soper & R. Homewood provided assistance with video scoring and Pernod Ricard NZ (C. Monk) provided electrical assistance.

CHAPTER FIVE

TRANSLOCATION OF THREATENED NEW ZEALAND FALCONS TO VINEYARDS INCREASES NEST ATTENDANCE, BROODING, AND FEEDING RATES

Three New Zealand falcon chicks (~1-2 days old) in a nest in the hills of Marlborough. (Photo: S. Kross).

Kross, S.M., Tylianakis, J.M. & Nelson X.J. 2012. Translocation of threatened New Zealand falcons to vineyards increases nest attendance, brooding and feeding rates. PLoS ONE 7(6): e38679. doi:10.1371/journal.pone.0038679

ABSTRACT

Anthropogenic habitats can be rich in resources, and may in some cases provide potential habitat for species whose natural habitat has declined. Some native species may even provide ecosystem services for agriculture, though maladaptive behaviour may prevent species from thriving in a new agricultural habitat. We used remote videography to assess the conservation value of a translocation project that reintroduced individuals of the threatened New Zealand falcon (*Falco novaeseelandiae*) into a highly modified agricultural habitat. Over 2,800 recording hours of footage was used to describe the breeding behaviour of the New Zealand falcon and to compare the behaviour of falcons living in six natural nests in the hills with that of four breeding falcon pairs that had been transported into vineyards. Falcons in vineyard nests had higher nest attendance, higher brooding rates, and higher feeding rates than falcons in hill nests. As chick age increased, parents in vineyard nests fed chicks a greater amount of total prey and larger prey items on average than did parents in hill nests. Parents with larger broods brought in larger prey items and a greater total sum of prey biomass. Nevertheless, chicks in nests containing siblings received less daily biomass per individual than single chicks. Some of these results can be attributed to the supplementary feeding of falcons in vineyards. However, even after removing supplementary food from our analysis, falcons in vineyards still fed larger prey items to chicks than did parents in hill nests, suggesting that the anthropogenic habitat may be a viable source of quality food. Although agricultural regions globally are rarely associated with raptor conservation, these results suggest that translocating New Zealand falcons into vineyards has potential for the conservation of this species.

INTRODUCTION

Agricultural expansion and intensification is a principal contributor to habitat change (Foley et al. 2005) and represents the "greatest extinction threat to birds" (Green et al. 2005). Raptor species worldwide have suffered declines (Butchart et al. 2004), largely as a result of anthropogenic activities linked with agriculture, such as land clearing and the use of poisons for pest control (Ratcliff 1967). Additional causes of mortality include persecution as a result of human-wildlife conflict and electrocution on electro-utility structures (Lehman et al. 2007; Thirgood & Redpath 2008; López-López et al. 2011).

Raptor declines can be mitigated through the reintroduction of individual birds from their strongholds in order to bring threatened species back to their historic ranges (Moore et al. 2008), and this method has been successfully used to expand the ranges of a number of threatened raptors worldwide (Cade 2000; Negro et al. 2007). However, release sites for such reintroduction programs normally comprise regions of natural habitat from which raptors have become extirpated. With land increasingly being put to use for anthropogenic purposes, there is inevitably a conflict when land is set aside for conservation. Consequently, there have been calls for increasing biodiversity conservation outside of the traditional reserve system (Fischer et al. 2011). These suggest that conservation efforts could be incorporated within primary production systems (Edwards & Abivardi 1998; MacLeod et al. 2008) by using farming practices that are more wildlife-friendly (Green et al. 2005).

Conservation scientists have traditionally been slow to incorporate animal behaviour when developing sustainable conservation management plans and policy (Knight 2001; Berger-Tal et al. 2011). There is considerable variability in how well raptors adjust to human landscapes, with some species being unable to inhabit modified habitats while others show considerable flexibility in this regard (Bird et al. 1996). The ability of translocated individuals to display natural behaviour can influence the success of reintroduction projects (Moore et al. 2008; Knight 2001; Armstrong & Seddon 2008), and the need to assess the behavioural ramifications of translocation is particularly acute when animals are reintroduced into anthropogenic landscapes.

In Marlborough, New Zealand's largest wine-growing region, there is an intensive monoculture of vineyards spread throughout the valleys that were once inhabited by the now

threatened New Zealand falcon (*Falco novaeseelandiae*; Miskelly et al. 2008), the country's only remaining endemic bird of prey. To combat the decline of falcons in Marlborough (Gaze & Hutzler 2004) a project called 'Falcons For Grapes' (FFG) was established in 2005 to reintroduce falcons into the vineyard-dominated valleys. As its name suggests, this project aims to use falcons to benefit the wine industry through their release into vineyards, while at the same time benefitting falcons through access to higher prey densities in vineyards and an expansion of their range (MAF 2009b). Although vineyards have high densities of potential vertebrate prey (particularly European birds), falcons relocated to vineyards are also enticed to stay through supplementary feeding schemes. Recent work has shown that falcon presence in vineyards is associated with considerable economic savings through a reduction in grape damage caused by passerine pest birds (Chapter 2). However, whether there is a simultaneous benefit to the falcon population is, as yet, unknown. The FFG project presented us with a unique opportunity to do a comparative analysis of the breeding behaviour of reintroduced falcons in vineyards with falcons found in the nearby hills. In particular, we use these comparative data to investigate an important aspect of the FFG's strategy: namely, whether reintroduction of falcons into vineyards holds promise for the conservation of *F. novaeseelandiae*.

New Zealand falcons evolved in the absence of land-dwelling mammals, and therefore lack the morphological and behavioural adaptations necessary to deal with mammalian predators (Wilson 2004). For example, they often nest in 'scrapes' on the ground, making them prone to high levels of nest predation (Fox 1977; Seaton et al. 2009; Chapter 7). Generally, raptor species share biparental care duties during incubation and when their altricial chicks first hatch (Newton 1979). Extrinsic factors, such as habitat quality and prey abundance, may influence the time budget allocated by raptors to different activities and thus potentially affect breeding success (Palmer et al. 2001).

Despite its threatened status, little is known about the breeding behaviour of the New Zealand falcon. Falcon chicks grow quickly and this necessitates that adult falcons provision them with a large amount of prey each day. Parents must therefore balance the need to feed their young against the increased exposure of young to potential nest predation while their parents are foraging. Areas of high prey density may therefore benefit falcons considerably through a reduction of time spent searching for prey. This is particularly relevant in

Marlborough, as prey density in vineyards appears to be somewhat higher than that available in the surrounding hillsides, possibly as a consequence of the ready availability of prey species in the grape-filled valley floor (Chapter 4). Here, by examining how the parental behaviour of the New Zealand falcon differs between hill and anthropogenic vineyard habitats, we provide further evidence that behavioural studies should be inextricably tied to the implementation of sustainable conservation management plans.

METHODS

Study Species

In the New Zealand falcon, incubation lasts for 30 days, followed by a 30-35 day rearing period during which chicks develop the ability to thermoregulate (at approximately 12 days), reach full adult weight (at approximately 20 days), and develop feathers. Adult females typically undertake the majority of nest attendance, nest defense, and feeding of chicks, while male falcons assume most of the foraging and provision females and chicks with food (Fox 1977). As chicks grow, female falcons begin to take part in foraging and food provisioning (Fox 1977).

Falcon nests were located by interviewing local farmers and forestry workers. Non-vineyard falcon nests ('hill nests') were found either in hillside forestry plantations (*Pinus radiata*) or in steep-sided valleys dominated by a mix of native and introduced grasses and dense scrub (Chapter 3). In contrast, vineyard falcon nests ('vineyard nests') were near the valley floor, usually within a vineyard, although occasionally within forestry plantations adjacent to a vineyard. The key differences were that vineyard adults were provided daily with one-day-old poultry chicks as supplementary food on an *ad hoc* basis, and that falcons nesting in vineyards had their nests raised from the ground into artificial nests in order to reduce the chances of predation by invasive mammals. Over 50 falcons have been released by the FFG project in the valleys of Marlborough between 2005 and 2011, and eight have been confirmed to breed within the vineyard region. including the nearby foothills (R. Seaton, personal communication).

Data collection

Our data were based on footage obtained from six hill nests (101 days or 1473 recording hours) and four vineyard nests (88 days or 1333 recording hours) monitored between 2008 and 2011.

We used a portable remote videography system with a near-infrared camera placed at the edge of the nest or mounted to the side of nest barrels in the case of vineyard nests. The system was set to record (at 30 fps) based on a motion-detection threshold of 10-15%, and has been shown to lose only 12% of potential recording hours, primarily due to battery failure or camera dislodgement (Chapter 3). For these data, if over 50% of recording hours in any given day were missed, that day was excluded from the dataset. Video was reviewed using Quick-Time Player (version 7.6.4; Apple Inc, Cupertino, CA, USA) at a maximum of four times normal speed to a minimum speed of frame-by-frame, allowing quick review of non-important files and detailed review of important events, such as feeding.

Monitored nests during the incubation stage had either 3 or 4 eggs in them, and monitored nests during the chick rearing stage had 1, 2, or 3 chicks. The number of chicks in these nests did not differ significantly between hill (n = 13) and vineyard (n = 8) nests (Mann Whitney U = 12.0, P = 0.91; for both habitats median = 2.0; 1st and 3rd quartiles are 1.0 and 3.0). In the rare (i.e. < 10% of recordings) cases where one or more of the chicks had moved outside of the recording area, we stipulated that at least one chick had to be fully visible to the camera to be included in the dataset. We also pooled data across nests that were recorded during the egg incubation stage of the breeding cycle from two vineyard and one hill nest in order to obtain data on attendance and incubation rates (485 recording hours).

We recorded the duration of parental behaviours (see Table 5.1) by scoring the start and end time of each behaviour, and used these numbers to calculate duration. In all cases we recorded the sex of the individual engaged in the behaviour. We estimated the biomass of each item that was brought into the nest by comparing the size of the prey item with previous, positively identified prey items, and the size of the adult falcon carrying the prey. The one-day-old poultry chicks provided as supplementary food were easily identifiable due to their bright yellow colour, and were identified in all cases when they were delivered to chicks. Additionally, we recorded the number of nest disturbances by people or other animals per day, and used an ordinal scale of 0-10 (with 10 being the highest and equivalent to something entering the falcon's nest) to measure the level of each disturbance to the nesting falcons (Table 5.1). The disturbances were considered to be additive per day; for example, if a nest was entered two times in one day, the disturbance level for the day would be equal to 20.

Table 5.1. Parental behaviour recorded at each falcon nest.

Behaviour	Description	Data obtained for analysis
Nest attendance	Time spent by adults in the nest, including being engaged in all of the behaviours below, as well as when in the nest, but not touching chicks or engaging in other defined behaviour.	Proportion of the daily total(s).
Nest activity	Number of times adult falcons departed the nest; used as a proxy for activity at the nest entrance (see Daan et al. 1996).	Counts.
Brooding/ Incubating	Adult falcon is physically touching at least one chick or egg with breast, tail, or wings. Also applies if falcon is standing over chicks to provide shade (stress brooding).	Proportion of the daily total(s). Count of incubating bouts. Average length of incubating bouts.
Nest maintenance	Adult falcon is pulling at substrate within scrape. Also applies to removing items such as prey remains.	Proportion of the daily total(s).
Feeding	Adult falcon is feeding food to chicks or is eating.	Proportion of the daily total(s). Counts of feeding events. Average time (s) between feeding events. Average biomass (g) of individual prey items. Sum of prey biomass (g)

We collected information on the amount of prey handling that occurred prior to items being delivered to the nest by the parents. Avian prey were aged according to feather structure: birds with completely sheathed feathers were considered nestlings, those with partially sheathed feathers were considered fledglings, and those with unsheathed feathers were considered adults (Lewis et al. 2004). The amount of prey handling done prior to parents delivering the item to chicks was noted, with prey being either completely plucked (no wing or tail feathers remaining), partially plucked (some wing or tail feathers remaining) or not plucked (all wing and tail feathers intact). We also noted the presence or absence of the preys' head at the time of delivery to the nest.

Data analysis

Data from individual nests were analysed with increasing chick age in days as a predictor variable, defined using the hatching date as chick age 0. In order to maximize data collection for all chicks, data were collected until day 30; the age at which chicks begin to fledge from the

nest (Fox 1977). Daily data recording began at 05:00 and ended at 21:00. These times were chosen because feeding events never occurred prior to 5 am, and out of a total of 2026 feeding events recorded, only 11 occurred after 9 pm (i.e., 99.5% of feeding events occurred during these hours).

We examined parental time budgets by calculating the proportion of the recorded daylight hours adult falcons spent in attendance at the nest, incubating/ brooding chicks, performing nest maintenance, or feeding chicks. These data were then transformed using an arcsine square root transformation, and modelled using generalised linear mixed effects models (GLMMs) with Gaussian error terms in the lme4 package (Bates et al. 2008) in R v. 2.7.2. (R Core Development Team 2008). We were unable to use binomial errors because our proportion time data were not derived from proportions of successes/failures in a fixed number of independent binary trials. Separate models were analysed for male and female adult falcons, except in cases where the proportion of a particular activity performed by the female versus the male were examined. The average length of incubation bouts, the average time between feeding events, the average biomass of prey items, and the average total biomass fed to chicks per day were all modelled using GLMMs with Gaussian errors. Counts for the amount of nest activity, the number of incubating bouts, the number of feeding events, and the level of disturbances per day were all modelled using GLMMs with Poisson errors. Feeding data were analysed first including items identified as supplementary food, and then excluding items identified as supplementary food.

Site (i.e. nest identity), the identity of the female and of the male parent were fitted as random effects in all GLMMs. The identity of the parents was included as random effects to control for non-independence of data between nests containing the same individual male or female falcon (across years, no two nests contained the same pair of adult falcons, but in a few cases either a male or female was paired with a different mate at a different nest site location). We included habitat type, the number of chicks in the nest, and level of disturbances as categorical fixed effects in the models. Chick age in days was included as a continuous fixed effect in the models. We also included an interaction term between chick age and habitat type, as well as second- and third-order polynomial terms for chick age in the models to account for potential nonlinear effects of chick age (e.g., asymptotes or step-changes in behaviour once a threshold age is reached).

Models were simplified by removing non-significant polynomial and interaction terms then main effects until model fit (measured using the Akaike Information Criterion, AIC) was maximized. We tested all models for evidence of overdispersion (on the basis of the ratio of residual deviance to degrees of freedom) and re-fitted overdispersed models using penalized quasi likelihood (the 'glmmPQL' function) in the MASS package (Venables & Ripley 2002) in R. For models fitted using Gaussian errors that did not show evidence of overdispersion, we used a Markov chain Monte Carlo (MCMC) resampling method with 10,000 simulations to estimate *P* values for the fixed effects (carried out using the 'pvals.fnc' function in the LanguageR package in R; Baayen 2008). In our results, where relevant, we present the mean (± SD) for untransformed data (as a measure of effect size) in addition to *P* and ± SEM values from model estimates.

RESULTS

Parental time budgets in each category all changed with chick age, and the amount of time spent feeding was also affected by habitat type. The effect of chick age on many of the response variables was nonlinear, evidenced by a significant quadratic (second order polynomial) term in the models for the proportion of the day spent feeding, average time between feeding bouts, the total daily biomass fed to chicks, nest activity, and the average length of incubation bouts, and both the second and third order polynomial terms being significant in the models for nest attendance and brooding. The number and level of nest disturbances did not differ significantly between the two habitats (t_6 = -0.51, P = 0.63) and was only significant (see below) in the model for the proportion of feeding done by females.

Incubation

During egg incubation, at least one adult falcon was present within the nest for 99.44 ± 0.61% of recorded hours (intercept for time present: t = 19.16, $P < 0.001$), and this did not change as egg age increased (t = -1.20, P = 0.24). There was a significant difference between the sexes in egg incubation (t = 7.76, $P < 0.001$), with females being responsible for 69.68 ± 1.61% of egg incubation. Model estimates indicate that female falcons performed an average of 8.81 ± 1.32

incubating bouts per day, and that as eggs approached hatching stage, females increased the number of incubating bouts per day by 0.21 ± 1.01 ($t = 2.05$, $P < 0.05$). As chicks aged, females also decreased the average length of incubating bouts, although this decrease was nonlinear (effects of egg age and second order polynomial term $P < 0.05$ in both cases). Nests with four eggs tended to have more incubating bouts ($t = 2.17$, $P < 0.05$), which were shorter on average ($t = -2.48$, $P < 0.05$), than nests with 3 eggs. Male falcons had a similar average number of incubating bouts to females (mean of 8.25 ± 1.11 bouts per day; this did not differ significantly with chick age (removed from model) or number of eggs in the nest ($t = 7.13$, $P = 0.09$)). However, male incubation bout lengths were on average shorter than female incubation bout lengths (mean incubation bout females 2389 ± 181.71 s; males 1869 ± 162.33, $t = 5.56$, $P < 0.001$).

Chick-rearing behaviour

In both habitat types, adults significantly decreased nest attendance as chicks aged ($t = -21.84$; $P < 0.001$; proportion of the day attending was: hill, 0.58 ± 0.44; vineyard, 0.67 ± 0.45), with the rate of this decline tending to slow after chicks reached approximately 20 days old (second and third order polynomial terms $P < 0.001$; Fig. 5.1). Nevertheless, parents in hill nests tended to have lower nest attendance than in vineyards ($t = -2.38$, $P < 0.05$, Fig. 5.1). This effect was largely due to the behaviour of female parents, which were responsible for the majority of nest attendance over the chick-rearing period (Fig. 5.1).

Parents were significantly more active in vineyard nests ($z = -4.13$, $P < 0.001$), leaving the nest more frequently (21.84 ± 8.12 daily nest exits) than in hill nests (17.10 ± 6.01 daily exits). When chicks first hatched, parents in vineyard nests averaged 33.6 nest exits/day, while those in hill nests averaged 26.05 nest exits/day. However, as chick age increased, parents in both habitats significantly decreased activity around the nest ($z = -10.83$, $P < 0.001$). This effect was nonlinear, with the amount of activity dropping off steeply after chicks reached approximately 11 days old (second order polynomial, $P < 0.001$).

There was no effect of habitat on the time spent brooding chicks ($t = -0.23$, $P = 0.72$; hill, 0.27 ± 0.36; vineyard, 0.29 ± 0.37 of the proportion of the day). In both habitat types, adults significantly decreased their time spent brooding as chicks aged ($t = -22.23$, $P < 0.001$),

although this effect was nonlinear, with the slope of the decline levelling out at close to zero once chicks reached approximately 18 days old (second and third order polynomials $P < 0.001$ in both cases).

There was no effect of habitat on the small proportion of the time per day spent maintaining nests (hill, 0.01 ± 0.02; vineyard, 0.01 ± 0.01) and the habitat term was removed from the simplified model. In both habitat types, adults significantly decreased the time spent maintaining nests as chicks aged ($t = -12.74$, $P < 0.001$).

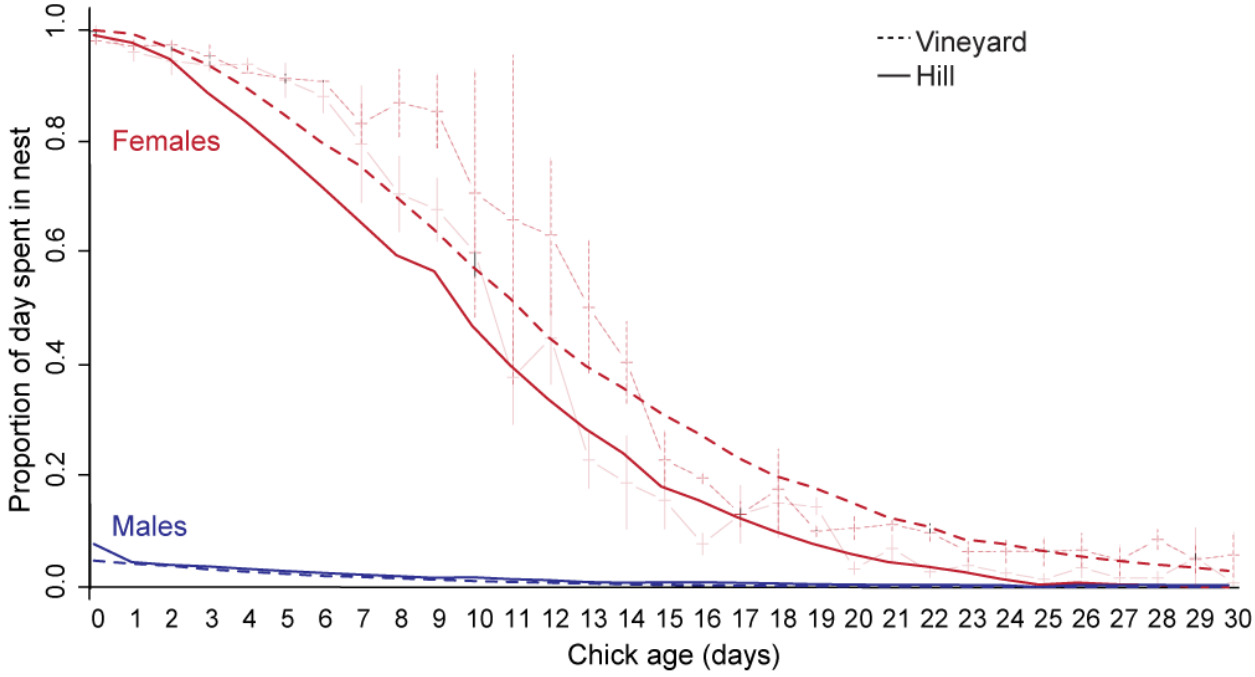

Figure 5.1. Proportion of the day that both adult falcons are in attendance at the nest as chick age increases in vineyard (dotted green lines) and hill (solid brown lines) nests. The thin light green and brown lines show the raw data for both parents combined ± SEM. Thick lines show the fitted values from a GLMM including significant second and third order polynomial terms for female falcons and from a GLMM including significant second order polynomial terms for male falcons.

Feeding behaviour

The supplementary food provided to vineyard falcons represented 17.89% ± 8.94% of prey items adults provisioned to their chicks. At three of the vineyard nests, supplementary food items represented <10% of the prey items brought to chicks. However, at the fourth nest, supplementary food items represented 44.53% of prey items brought to chicks.

Falcons from nests in the hills spent a significantly lower proportion of their time feeding chicks (t = -1.79, $P < 0.05$) than did falcons nesting in vineyards (hill, 0.05 ± 0.03; vineyard, 0.07 ± 0.03; Fig. 5.2). Females did 99.3% of the feeding, significantly more than the males (t = 14.80, $P < 0.0001$). Feeding decreased as chicks aged (t = -2.81, $P < 0.01$), although more so in hill nests than in vineyard nests (Habitat x chick age interaction: t = -3.33, $P = 0.001$; Fig. 5.2). In hill nests, parents increased the proportion of the day spent feeding from chick hatching until chicks were approximately 9 days old, after which they began to decrease the proportion of the day spent feeding. In vineyard nests, this switch occurred later, when chicks were approximately 12 days old (second order polynomial term $P < 0.001$). Nest disturbances also had a significant negative effect on the proportion of feeding done by the female (t = -3.80, $P < 0.001$) in both nest types.

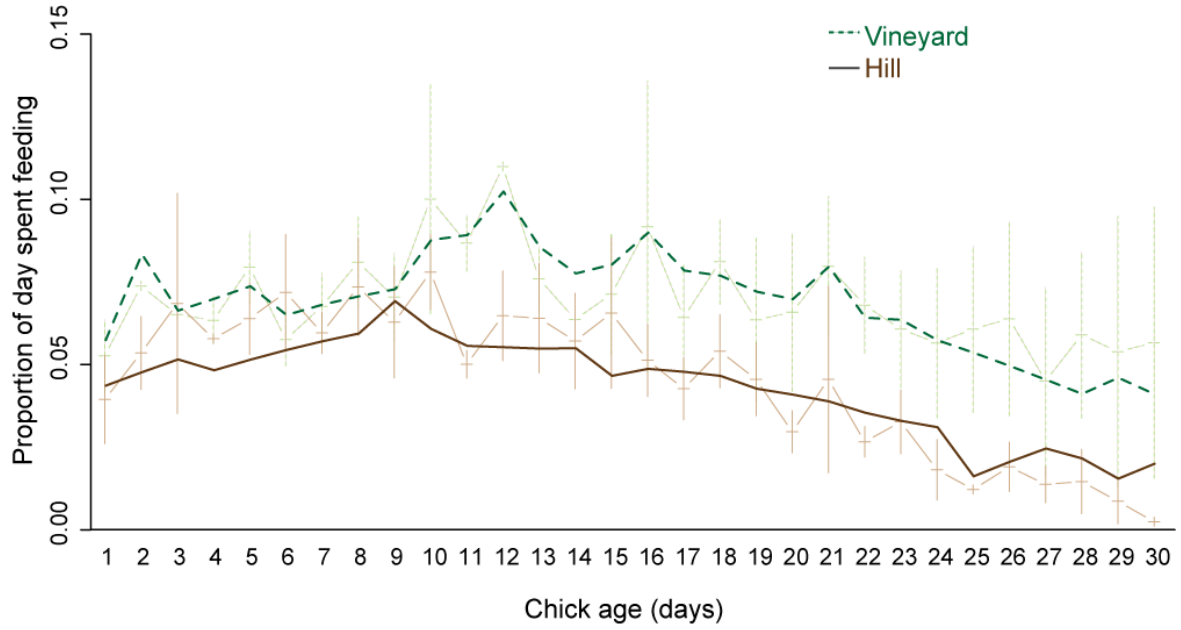

Figure 5.2. Proportion of the day that parents spent feeding chicks in vineyard and hill nests. Dark lines are the fitted model estimates from a GLMM with a second-order polynomial fitted for chick age. Pale lines are raw data (+/- SEM). Falcons in vineyard nests spent a significantly greater proportion of the day feeding chicks compared with falcons in hill nests ($P < 0.05$).

Vineyard and hill nests did not differ significantly in the interval between feeding bouts (t = 1.49, $P = 0.19$; hill, 4998 ± 1768 s; vineyard, 4814 ± 1813 s). Regardless of habitat type or

chick age, nests containing a greater number of chicks experienced less time between feeding bouts (2 chick nests: $t = -3.00$, $P < 0.05$; 3 chick nests: $t = -8.12$, $P < 0.001$). In both habitats, as chick age increased, male falcons delivered more food items to the chicks ($t = 9.36$, $P < 0.001$), starting at an average of 0.05 feedings per day when chicks first hatched and increasing by 0.15 feedings for each day as chicks aged. Female falcons in vineyard nests also increased their number of feeding events as chick age increased ($t = 2.40$, $P < 0.05$), starting at an average of 7.75 feedings per day when chicks first hatched and increasing by 0.07 feedings per day as chick age increased. In contrast, females in hill nests started at the same average number of feeding events as their vineyard counterparts, but decreased the number of feedings by 0.07 per day as chick age increased ($t = -3.03$, $P < 0.005$). The second order polynomial term was removed from the model for number of feeding events by female falcons, so these relationships were linear. When supplementary food was excluded from the analysis, nests in the hills had an average of 1.20 more feeding events per day ($t = 3.14$, $P < 0.02$) compared with vineyard nests. Removing supplementary food from the analysis did not change the fact that, compared with nests with one chick, nests containing 2 chicks ($t = 2.94$, $P < 0.05$) and 3 chicks ($t = 5.61$, $P < 0.001$) received more food (2.84 and 3.05 more feeding events per day, respectively). Both the quadratic and cubic polynomials for chick age were retained in the final model, suggesting a nonlinear relationship.

At the time of hatching, there was no effect of habitat type ($t = 1.21$, $P = 0.26$) on the average biomass of each individual prey item consumed by chicks (hill, 22.23 ± 6.52 g; vineyard, 22.96 ± 8.59 g). However, as chick age increased, the average biomass of prey items in both habitats increased ($t = 2.91$, $P < 0.005$), and this increase was greater in vineyard nests than in hill nests (chick age x habitat interaction, $t = -2.72$, $P < 0.05$). Excluding supplementary food from this analysis reduced the average biomass slightly in vineyard nests (21.15 ± 8.84 g) at the time of hatching, but there remained no significant effect of habitat type in our model ($t = 1.86$, $P = 0.10$). However, as chick age increased, even without including supplementary food in the analysis, the average biomass of prey items in vineyard nests increased ($t = 3.04$, $P < 0.005$) but in hill nests decreased (chick age x habitat interaction, $t = -2.80$, $P < 0.05$).

Considering all prey items summed together, when chicks first hatched there was no difference in the total biomass fed to them in the different habitat types ($t = 0.44$, $P = 0.68$), but as chicks became older, there was an increasing difference between hill and vineyard nests, with

vineyard nest parents feeding chicks an additional 5.53 g per day (Chick age effect: $t = 3.41$, $P < 0.001$), while parents from the hill nests only fed an additional 0.43 g per day (habitat x chick age interaction: $t = -3.78$, $P < 0.001$; Fig. 5.3). Nests with more chicks were also given more food. Keeping all other variables constant, nests with 1 chick received a daily mean ± SEM of 129.73 ± 37.54 g ($t = 3.46$, $P < 0.001$), those with 2 chicks 288.44 ± 52.50 g ($t = 3.02$; $P = 0.02$), while those with 3 chicks received 281.12 ± 25.38 g ($t = 4.82$, $P < 0.0001$) of food. Excluding supplementary food items from the analysis for total biomass brought to chicks removed the significance of the chick age x habitat interaction ($t = -1.81$, $P = 0.07$, and there remained no statistically significant main effect on the total biomass fed to chicks ($t = 2.42$, $P = 0.05$). Disregarding supplementary food did not change the effect of number of chicks in the nest on total biomass.

A greater proportion of the bird prey delivered to vineyard nests were completely plucked (70.38 ± 2.97%) compared with hill nests (56.10 ± 3.92%, $t_8 = 2.90$, $P = 0.02$). Hill falcons brought their chicks a greater number of partially plucked (21.48 ± 2.88%) and unplucked (17.08 ± 4.54%) avian prey compared with vineyard falcons (15.67 ± 2.96% and 12.32 ± 2.41% respectively) although these differences were not statistically significant (partially plucked: $t_{7.4} = 1.41$, $P = 0.2$; not plucked: $t_{7.3} = 0.92$, $P = 0.4$). Falcons in vineyard nests decapitated more of the prey items delivered to chicks (68.59 ± 3.29%) than falcons in hill nests (56.31 ± 2.22%, $t_{5.7} = 3.10$, $P = 0.02$). Only 42.45% of prey items delivered to nests were identified to age class. The diet of falcons in vineyards consisted of a higher proportion of juvenile avian prey (vineyard mean= 5.19 ± 1.94%, hill mean= 1.28 ± 0.73%, $t = 3.86$, $P = 0.02$), but the two habitats were similar in the proportion of adult (mean= 27.98 ± 11.27%, $P > 0.30$) and nestling (mean = 10.91 ± 5.23%, $P > 0.80$) prey items in the diets fed to chicks.

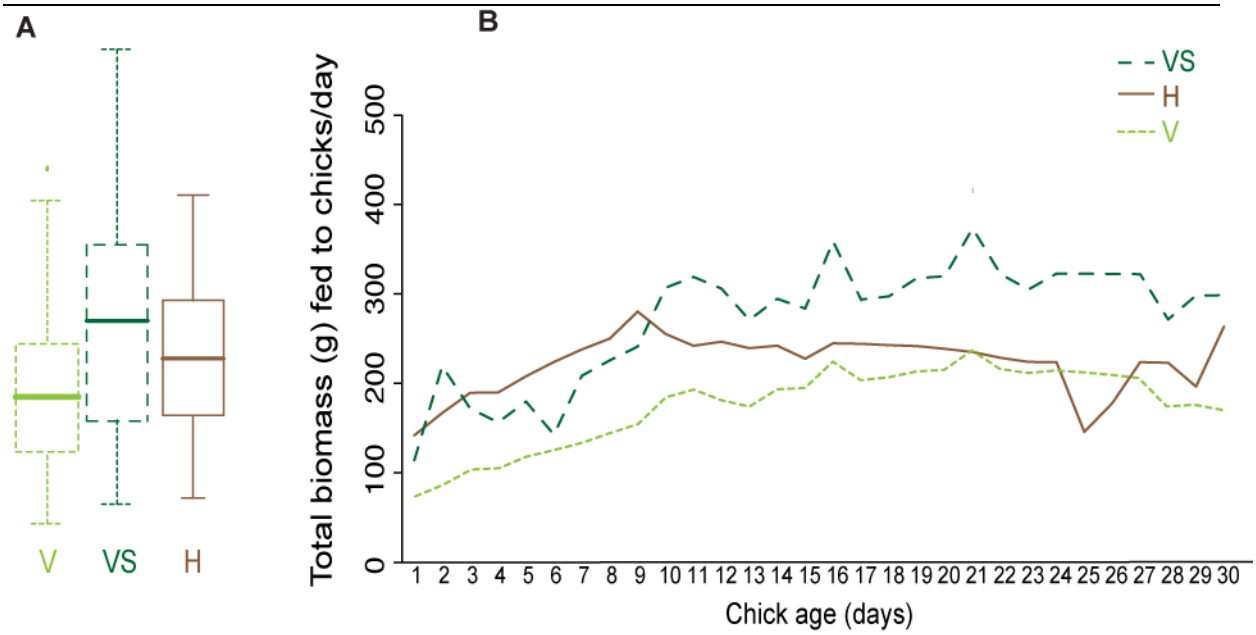

Figure 5.3. The total biomass of prey brought into nests in vineyards and hills. **A** The minimum, lower quartile, median, upper quartile, and maximum observations for vineyard nests with supplementary food items excluded (V), for vineyard nests including supplementary food items (VS) and for hill nests (H). **B** The fitted model estimates from a GLMM with a significant second order polynomial fitted for chick age, including supplementary food for vineyard nests (VS) and excluding supplementary food (V). Model estimates indicated that as chick age increased falcons in vineyard nests brought in more total prey each day than did falcons in hill nests ($P < 0.001$).

DISCUSSION

Reintroducing the New Zealand falcon into the vineyards of Marlborough has previously been shown to successfully provide vineyards with a natural form of pest control, by reducing the abundance of pest birds and the amount of damage found on vineyard grapes (Chapter 2). However, without evidence of a benefit to the falcons themselves, the effort and cost of translocating individuals of this threatened species to vineyards may be unjustified. Our results show that, within an intensive agricultural area, falcons are in fact capable of better parental care and chick feeding than in their normal habitat. In addition to spending more time attending and feeding their chicks, vineyard falcons provided better quality food. They provided significantly more plucked and decapitated prey to their nestlings. By completely removing these indigestible food parts, parents provide chicks with food items that are more energy efficient to digest, that potentially reduce the risk of ectoparasite exposure to chicks and that may reduce the chances of attracting predators to the nest by avoiding a build-up of prey remains around the nest area (Rands et al. 2000). Falcons in vineyards had higher nest attendance, spent more time feeding chicks, and fed chicks more often and with more food compared with falcons in hill nests. While the differences observed between habitats in this study may have been due in part to the supplementary food provided to the falcons living in vineyards, removing these feeding events from our models still indicates that falcons living in vineyards are at least as good, if not better, at provisioning nestlings with food as those in the hills. Furthermore, removing the supplementary food from our analysis revealed that falcons in vineyards tend to increase the size of average prey items as chick age increases, whereas those in the hills actually catch smaller prey. Therefore, removing these data provides a highly conservative estimate of differences between the habitat types, as vineyard falcons would likely find other food if supplementary food was unavailable. Further experimentation into the effect of supplementary food on falcons in the vineyards will provide the link necessary to distinguish the quality of the two habitats for falcons. Our results provide evidence that New Zealand falcons are capable of displaying the behavioural plasticity necessary to survive and rear their offspring in a highly altered anthropogenic landscape. This concurs with recent results that suggest that this species is capable of nesting in *Pinus radiata* plantation forestry (Seaton et al.

2009), whereas forestry habitat was previously thought to be deleterious to the falcon (Fox 1977).

Reproduction is an energetically costly phase in the annual cycle of all breeding birds, and a lack of food over any portion of the reproductive cycle can have limiting effects on both parents and their offspring (Martin 1987; Daan et al. 1996). Nesting birds of prey must balance the relatively low-cost behaviours of caring for their young in the nest (activities such as incubating and brooding) with the need to forage away from the nest - a behaviour high in metabolic cost. The availability of prey in the areas surrounding the nest therefore has a direct effect on the breeding success of raptors, as is the case with peregrine falcons (*Falco peregrinus*), where increased nest attendance by females is associated with increased nesting success (Palmer et al. 2001). Providing supplementary food to altricial birds during breeding can therefore positively affect reproduction rates, fledging condition and parent survival (Newton & Marquis 1981; Martin 1987; Salafsky et al. 2007). Similarly, areas of high prey densities are associated with higher reproductive rates (Martin 1987; Salafsky et al. 2007). In our study area, vineyards have a higher density of avian prey compared with hills (Chapter 4), and falcons were additionally provided with supplementary food. It is therefore difficult to tease out the effect of habitat alone, or supplementary food alone, on nesting falcons. While some other raptors (i.e. Eurasian kestrels, *Falco tinninculus*; Wiehn & Korpimäki 1997) have been shown to benefit from supplementary feeding, our results go further, showing that supplementary feeding alone does not fully explain the positive ramifications that we have demonstrated for vineyard habitat.

Females were present within the nest for much more of the day than males. Females therefore took on the majority of the nest-based behaviours that were the focus of this study, and it is likely that males took on the majority of foraging, and provisioned females with prey items with which to feed chicks. This most likely occurs because female falcons, as the physically dominant individual in a pair, remain within or near the nest, and intercept males approaching with food in order to feed the chicks themselves, especially prior to chicks being able to thermoregulate, a pattern that has been shown in the peregrine falcon (Carlier & Gallo 1995). If males were unable to forage efficiently and females were forced to forage in order to provision chicks, especially when chicks were not yet able to thermoregulate, this could result in lower nesting success. In our study, supplementary food was only relied upon as a food

source by one of the vineyard pairs: the remaining 3 pairs used supplementary food for <10% of their feedings. Interestingly, in these 3 pairs, 98.25% of the supplementary food items were brought to the nest after chicks had reached 14 days of age, by which time adult females had drastically reduced the amount of time they spent in the nest (Figure 5.1) and were likely to have joined their mates in foraging and food provisioning. Male kestrels have been shown to avoid provisioning their chicks with supplementary food items, whereas females feed both themselves and their chicks with supplementary food when it is available (Wiehn & Korpimäki 1997), and our results indicate that it is possible this is also the case in New Zealand falcon.

Parents in nests with more chicks fed their chicks a greater total biomass per day, and fed them more often. However, these increases did not fully compensate for the sharing of food items amongst chicks. On average, single chicks received more food per day (174 g), than each of two chicks (131 g) or three chicks (97 g), and this effect remained even after removing supplementary food from the analysis. These results indicate that removing chicks from hill nests (as carried out by the FFG project) may benefit the remaining chick through increased food provisioning. However, this assumption does not take into account the behavioural impact of removing siblings on the remaining chick (Hudson et al. 2011), or the impact of this harvest of individuals on the falcon population in the hills (Armstrong & Seddon 2008).

One important caveat to the conservation implications of this study is mortality as a consequence of electrocution, which may increase due to the prevalence of power lines in anthropogenic habitats. There is some evidence (Fox & Wynn 2010; Appendix 2) to suggest that falcons residing in vineyards are suffering significant losses due to electrocution, a common pattern among raptors (Lehman et al. 2007). However, it has recently been demonstrated that if political will can be found, initiatives to mitigate these effects are both effective and affordable López-López et al. 2011).

Our results suggest that there is considerable potential in the idea of reintroducing falcons into vineyards. We have previously demonstrated significant economic benefits for vineyards containing falcons due to a reduction in damaged or destroyed grapes (Chapter 2). Here, we show that there may also be beneficial effects for falcons breeding within vineyards. Vineyard falcons tended to have greater access to food than falcons in the surrounding hills, enabling them to spend more time feeding and protecting their chicks. Experimentally providing only some of the vineyard falcons with supplementary food in the future will lead to

further understanding of the effect of habitat alone in the breeding behaviour of the threatened New Zealand falcon.

ACKNOWLEDGEMENTS

I am grateful to my supervisors Ximena Nelson and Jason Tylianakis for helping to plan these experiments and for providing essential feedback and comments on the analysis and writing of this chapter. For advice, assistance with locating nests and placing cameras we thank: C. Wynn, N. Fox, H. Oliver, L. Olley, P. Lintott, J. Cooper, J. Crowe, B. Coles, J. Knott, J. Kumagai, K. Morgan, X. Birch, R. Seaton, D. Harliwich and E. Soper. For access to land, we thank: Nelson Forests Ltd (D. Parsons), Winegrowers of ARA, Marisco Vineyards (R. Clare), M. Gifford, Spray Point Station (J & R Mapp), Richmond Brook Station, Wye Hills Farm (E & J Rentoul), as well as all landowners who provided access for falcon nest searches. E. Soper & R. Homewood provided assistance with video scoring and Pernod Ricard NZ (C. Monk) provided electrical assistance.

CHAPTER SIX

FACTORS INFLUENCING THE BEHAVIOURAL DEVELOPMENT OF JUVENILE NEW ZEALAND FALCONS

Juvenile falcon. (Photo: B. Kay-Coles)

Kross, S.M. & X.J. Nelson. Under Review. Factors influencing the behavioural development of juvenile New Zealand falcons.

ABSTRACT

Behavioural development during the post-fledging dependency period has significant ramifications on the survival rate of birds once they reach independence. During the post-fledging dependency period, adult raptors are thought to train their progeny in flight and hunting techniques, however, the importance of this parental teaching is relatively unknown. This lack of knowledge may impact the success of reintroduction projects where juveniles are released into areas with no adult presence, as commonly done in raptors. We examined the influence of parents, siblings, individual sex, habitat type, and age on the development of behaviour in the first four weeks after fledging in juvenile New Zealand falcons (*Falco novaeseelandiae*). We compared the behaviour of wild-reared falcons with the behaviour of juvenile falcons recently released as part of a conservation initiative. We used focal-animal sampling to determine the time spent engaged in, and frequency of, several behaviours relevant to survival and development, including: frequency and distance of flights, time spent perching, time spent walking on the ground, time spent playing, number of pursuits of conspecifics, and number of hunting attempts. All behaviours increased over time except for perching and walking on the ground, which decreased. Parental presence was associated with more hunting attempts, less time spent perching, and a greater proportion of conspecific pursuit flights. Juveniles with siblings flew more often, and had a greater proportion of conspecific pursuit flights. They also spent more time walking on the ground and engaged in more play behaviour. We suggest that, provided New Zealand falcons are released in groups, reintroduction of this threatened species does not have a major impact on the behavioural development of individuals.

INTRODUCTION

Hunting success is largely determined by a combination of innate and learned behaviour, but hunting skills can often be a product of one or other of these components. Although rarely acknowledged, innately derived hunting techniques can be exceedingly complex and flexible, as clearly demonstrated in the Salticidae, jumping spiders (Jackson & Nelson 2011; Nelson & Jackson 2011). That small-brained animals use innate tactics may not be a surprise, and the assumption is that larger animals rely more strongly on learning to develop behavioural phenotypes. Despite this, there is evidence of a strong innate component in the hunting techniques of several species of birds, such as common kestrels (*Falco tinnunculus*), which perceive UV reflectance in the scent marks of vole prey without experience, although this ability improves through learning (Zampiga et al. 2006). Similarly, painted redstarts (*Myioborus pictus*) use complex displays comprised of spreading the tail and wings while pivoting in order to flush insects from hiding by triggering escape responses (mis)directed toward the insectivorous redstart. These displays are innate, as is their context-dependant use based on habitat characteristics (Jabłoński et al. 2006).

Despite the importance of innate skills, experience with prey has been shown to increase individual hunting success in a variety of taxa, including the aforementioned jumping spiders (Edwards & Jackson 1994), salamanders (Gibbons et al. 2005), predatory fish (Reid et al. 2010) and birds (Pietrewicz & Kamil 1979). In addition to learning through direct experience with prey, hunting skills may be acquired through horizontal and vertical transmission, or learning through observation of siblings and parents, respectively (Edwards 1989; Lickliter et al. 1993; Ricklefs 2004). For example, wolf spiders (Lycosidae) raised with parents and siblings during early development have increased hunting skills and have larger brains compared to solitary spiders (Punzo & Ludwig 2002), while rats raised without parents or siblings show reduced social development (Lévy et al. 2003). For altricial birds that rely on parental care early-on in life, learning from conspecifics may play a vital role in development, either through increased competition (Michaud & Leonard 2000), or through greater environmental enrichment (Lickliter et al. 1993).

The post-fledging dependency period is an important, but understudied, stage in the development young birds. During this period, which can range in duration from weeks to

months depending on species, sex, and also on prey availability (Heinsohn 1991; Ricklefs 2004; Wiens et al. 2006), recently fledged birds rely on their parents for some or all of their food, while at the same time developing the flight, foraging, and social skills necessary for independent survival (Weathers & Sullivan 1989; Heinsohn 1991; Wheelwright & Templeton 2003; Arroyo et al. 2002; Yoda et al. 2004). This period also has implications for the development of cognitive ability and brain growth (Ricklefs 2004). Upon reaching independence, many avian species suffer high mortality rates, and the quality of behavioural development obtained during the post-fledging dependency period likely plays a role in the severity of these mortality rates (Heinsohn 1991).

Reintroductions are a popular tool in threatened species conservation, but this method often has low success rates (Fischer & Lindenmayer 2000). There have been indications that a lack of behavioural development due to reduced exposure to parents, siblings, and natural conditions, has led to lower survival rates in captive-reared and released individuals compared to wild-reared individuals, as found in hatchery-reared fish (*Scortum barcoo*; Reid et al. 2010), Vancouver island marmots (*Marmota vancouverensis*; Aaltonen et al. 2009), and aplomado falcons (*Falco femoralis*; Brown et al. 2006).

Raptor declines have been mitigated through the reintroduction of individual birds from their strongholds into areas of their historic ranges from which they have been extirpated (Cade 2000). Commonly, raptors are released using a method known as 'hacking', whereby juvenile birds are released in small groups from artificial nests around the time that they would normally fledge from a natural nest (Sherrod et al. 1982). The post-fledging dependency period in hacked individuals is particularly important, as these juveniles are without parents and therefore must be fed by humans in order to survive. This has potential implications on the development of vital behaviours such as flight and hunting, as adult birds are thought to participate in training of young birds by hunting within view of the nest and through aerial food passes (Newton 1979; Kitowski 2005).

In birds of prey, the importance of siblings in the development of flight and hunting behaviours is relatively unknown, although in ospreys (*Pandion haliaetus*), siblings developed complex hunting behaviour faster than single juveniles (Edwards 1989). With the exception of a few studies, the role of conspecifics on the development of behaviour in avian species is an overlooked topic (Lickliter et al. 1993), yet horizontal transmission of learned skills and play

behaviour between individuals may influence the speed of behavioural development (Ricklefs 2004; Kitowski 2005, 2009). Similarly, competition for resources may drive the development of behaviours such as flight and hunting (Bustamente & Hiraldo 1989; Heihnson 1991).

A reintroduction project of the threatened New Zealand falcon (*Falco novaeseelandiae*) provided us with the opportunity to examine the effects of parental and sibling presence on the behavioural development of young falcons in the post-fledging dependency period. We compared the behaviour of wild-reared falcons with that of recently released falcons using focal-animal sampling to determine the time spent engaged in several behaviours relevant to survival and development. We examined the influence of parents, siblings, individual sex, habitat type, and age on the development of behaviour in the first four weeks after fledging.

METHODS

Study animals and general methods

We chose the critical four weeks immediately following fledging (chick age 5-9 weeks) as a period in which to observe chicks, as this is the time when most flight and hunting behaviours develop (Lawrence & Gay 1991), and is prior to the onset of dispersal and independence (Seaton et al. 2008). Chicks at this age rarely leave the area immediately surrounding the nest scrape (a shallow depression that falcons dig in the ground under an overhanging rock or fallen tree; Fox 1977) and after 14 weeks of age it becomes difficult to locate chicks because of their expanding range (Lawrence & Gay 1991).

We spent 181 hours observing a total of 23 juvenile falcons. Observations were made at four natural nests with parents (henceforth: 'wild-reared' juveniles), and at six release sites where no parents were present (henceforth: 'released' juveniles). Wild-reared and released juveniles could be single birds, or part of a cohort of two or three siblings. Wild nests were located in remote locations in the rugged, and difficult to access, hills of Marlborough, a region at the top of New Zealand's South island. *F. novaeseelandiae* is a nationally threatened species (Miskelly et al. 2008), with a 4km^2 breeding territory in our study area (Fox 1977). Vineyard nests or release sites were located within or immediately adjacent to intensively managed vineyards in the valleys of the region.

We visited each site once per week for the four weeks immediately following natural fledging or release. All four natural nests were monitored with remote videography and so the exact time of fledging was known. We were informed of release dates by volunteers working for the release programme. Released juveniles were roughly the same age as those that were wild-reared, but may have been somewhat older (< 5 days). Nest and release sites were visited for a period of 3 h each week.

Observations were carried out within 5 h of sunrise or sunset and were not undertaken in high winds, heavy rain, or extremely warm weather (> 32^{o}C). If weather prevented observations, we returned to the same site later in the same week to carry out observations. Nonetheless, there were occasions when chicks could not be found or when poor weather prevented us from reaching a nest or release site in a given week. We were able to observe 16 chicks in their first week after fledging at 6 weeks of age (6 of which were wild-reared), 21 chicks in their 7th and 8th weeks of age (10 of which were wild-reared), and 17 chicks in their 9th week of age (6 of which were wild-reared).

Behavioural observations

We used focal animal sampling (Martin and Bateson 1993), noting the duration of each behaviour that lasted for >30 s. Measured behaviours are mentioned in the text in *italics*. Mean observation time for each individual was 145.0 ± 5.09 min (± S.E.M.) per observation session. We first noted whether the focal falcon was *perching* off the ground, *walking on the ground*, or *flying*. We then also noted if juveniles were taking part in *play behaviour* which was characterised by individuals (either alone or with siblings) generally pouncing on objects or siblings, grabbing at objects or siblings with their talons, and running and rapidly flapping their wings (Supplementary Video 5). *Play behaviour* generally took place while falcons were *walking on the ground*.

We noted the *distance* (m) of each flight as well as the accuracy and difficulty of each landing attempt made by juvenile falcons. We classified *landing difficulty* by the size and stability of perches, with perches scaled as follows: 1, the ground; 2, a large, flat surface such as a log or feeding tray; 3, a smaller stable surface such as a thick branch or vineyard post; 4, a thin relatively unstable surface such as a small branch; 5, a very unstable surface such as a twig or the very top of a pine tree. We further classified *landing accuracy* as follows: 1, landing not

accomplished; 2, partial landing but individual unstable and immediately took off or fell off perch; 3, landing accomplished but individual had to flap wings to balance or stumbled; 4, landing accomplished with steps needed to balance; 5, clean landing with no need for extra balancing.

We also noted if flights involved a *chase* of either a sibling or adult falcon (Fig. 6.1). Alternatively, if a juvenile took flight in pursuit of a heterospecific, these were considered as *hunting flights*. Hunting attempts varied from pursuits of invertebrates such as cicadas (*Hemiptera* spp.) to prolonged pursuits of flocks of birds such as starlings, *Sturnus vulgaris*.

We also measured the accuracy of *food passes* from adult falcons to juveniles on a scale of 1 to 5, as follows: 1, juvenile attempted to catch food but missed by over 1m; 2, juvenile within 1m of food but did not catch it; 3, juvenile made contact with food but did not catch it; 4, juvenile caught food poorly; 5, juvenile accurately caught food (Supplementary Video 5).

Figure 6.1. Still image taken from a video of a juvenile male New Zealand falcon (*Falco novaeseelandiae*) pursuing a juvenile female falcon in mock attack (see supplementary video 5 for examples of play behaviour).

Analysis

To standardise data from different observation periods, we determined the proportion of observation time for each individual spent perching, walking on the ground, and playing by dividing the total time spent engaged in each of these activities by the total observation time for

each focal individual per week, with week representing chick age. We also calculated the frequency of flights and hunting attempts that each individual made per minute of observation time per week. We modelled all data using generalised linear mixed effects models (GLMMs) in the lme4 package (Bates et al. 2008) in R (v.2.7.2; R core development team 2008). We used an arcsin square root transform on data for the number of flights and number of hunting attempts per minute of observation time and used a square root transform on data for mean flight distance, landing accuracy, and landing difficulty. We used a Gaussian family of errors to model our transformed data, and used a binomial family of errors to model our proportion data.

Because of our hierarchical sampling design, we included as random effects juvenile identification nested within nest or release site identification, in order to control for non-independence of samples from the same juvenile or from juveniles at the same site. Age (in weeks), presence of siblings, presence of parents, sex, and habitat type (either unmanaged hills or managed vineyards) were all included as categorical fixed effects in the models. We included interaction terms between two of the fixed effects in the models, and determined the most appropriate interaction term based on model fit (measured using the Akaike Information Criterion, AIC). We simplified models by removing non-significant interaction terms followed by main effects until model fit was maximised.

We tested all models for evidence of overdispersion (on the basis of the ratio of residual deviance to degrees of freedom) and re-fitted overdispersed models using penalised quasi likelihood (the 'glmmPQL' function) in the MASS package (Venables & Ripley 2002) in R. For models fitted using Gaussian errors that did not show evidence of overdispersion, we used a Markov Chain Monte Carlo (MCMC) resampling method with 10,000 simulations to estimate *p* values for the fixed effects, carried out using the 'pvals.fnc' function in the LanguageR package in R (Baayen 2008). In our results, where relevant, we present the mean (± S.E.M.) for untransformed data (as a measure of effect size) in addition to test statistics and *p* values.

RESULTS

Simplified model estimates are included in Table 6.1. Immediately after fledging (week 6), released juveniles spent a significantly greater proportion of time *perching* (0.87 ± 0.05) than wild-reared juveniles (0.45 ± 0.11; $t = 2.82$, $p = 0.03$). In weeks 7, 8, and 9 released juveniles

tended to decrease the proportion of time they spent perching (all $t < 1.9$, all $p > 0.1$), whereas over this same period wild-reared juveniles had a significant tendency to increase the proportion of time they spent perching (all $t > 2.6$, all $p < 0.02$; Fig. 6.2). Immediately after fledging there was a marginal (but non-significant) tendency for juveniles with siblings ($t = 1.84$, $p = 0.07$) and wild-reared juveniles ($t = 2.00$, $p = 0.09$) to spend more time walking on the *ground* compared with single and released juveniles, respectively (Fig. 6.3). In week 7, wild-reared juveniles decreased the proportion of time that they spent on the ground (all $t > 2.10$, all $p < 0.04$), whereas released juveniles increased the proportion of time spent on the ground ($t = 2.16$, $p = 0.04$), resulting in both released and wild-reared juveniles spending a similar proportion of time on the ground in weeks 8 and 9 (Fig 6.2).

Juveniles with siblings spent a greater proportion of the day engaged in *play* behaviour, (Fig. 6.3) although this did not reach significance ($t = 1.68$, $p = 0.10$). Juvenile age, presence of parents, and the interaction between juvenile age and presence of parents were retained in the model for time spent playing, but did not have significant explanatory value. Additionally, the presence of siblings had a non-significant tendency to increase the mean number of flights observed ($t = 2.75$, $p_{MCMC} = 0.08$).

Table 6.1. Summary of variables retained in the models for the measured behaviours.

Response variable	Model used	Data transforma-tion	Predictor variable	Estimate	SE	Test statistic	P value
Proportion of time spent perching	Quasi-penalised GLMM (Binomial)	None	Intercept	1.84	0.62	2.96	0.005
			Age 7	-0.67	0.52	-1.29	0.20
			Age 8	-0.95	0.51	-1.88	0.07
			Age 9	-0.92	0.51	-1.81	0.08
			Wild-reared	-2.24	0.79	-2.82	0.03
			Siblings	0.24	0.44	0.55	0.58
			Age 7: wild-reared	2.07	0.78	2.64	0.01
			Age 8: wild-reared	3.17	0.84	3.79	<0.001
			Age 9: wild-reared	3.13	0.86	3.64	<0.001
Proportion of time spent on ground	Quasi-penalised GLMM (Binomial)	None	Intercept	-4.15	1.35	-3.08	0.004
			Age 7	2.83	1.31	2.15	0.04
			Age 8	1.70	1.37	1.24	0.22
			Age 9	2.23	1.35	1.66	0.11
			Wild-reared	1.59	0.79	2.00	0.09
			Siblings	2.53	1.37	1.85	0.07
			Age 7: wild-reared	-1.58	0.72	-2.19	0.03
			Age 8: wild-reared	-2.13	0.81	-2.64	0.01
			Age 9: wild-reared	-3.64	0.85	-4.25	<0.001
			Age 7: siblings	-2.75	1.41	-1.94	0.06
			Age 8: siblings	-2.17	1.47	-1.47	0.15
			Age 9: siblings	-1.75	1.43	-1.23	0.23
Proportion of time spent playing	GLMM (Binomial)	None	Intercept	-5.26	0.54	-9.80	<0.001
			Age 7	0.55	0.25	2.15	0.03
			Age 8	0.27	0.27	1.00	0.32
			Age 9	-0.01	0.28	-0.02	0.99
			Wild-reared	1.13	0.59	1.90	0.06
			Siblings	0.93	0.42	2.19	0.03
			Age 7: wild-reared	-1.17	0.32	-3.63	<0.001
			Age 8: wild-reared	-0.28	0.32	-0.864	0.39
			Age 9: wild-reared	-1.28	0.39	-3.26	0.002
Frequency of flights	GLMM (Gaussian)	Arcsin square-root	Intercept	0.12	0.08	1.54	0.06
			Age 7	0.07	0.05	1.32	0.22
			Age 8	0.20	0.05	3.74	<0.001
			Age 9	0.21	0.05	3.94	<0.001
			Siblings	0.17	0.06	2.75	0.08
Mean flight	GLMM	Square root	Intercept	2.53	1.69	1.49	0.17

Response variable	Model used	Data transforma-tion	Predictor variable	Estimate	SE	Test statistic	P value
distance (m)	(Gaussian)		Age 7	0.92	1.56	0.59	0.42
			Age 8	7.20	1.53	4.70	<0.001
			Age 9	10.97	1.62	6.76	<0.001
			Vineyard habitat	1.22	1.92	0.64	0.40
			Age 7: vineyard	-0.02	1.76	-0.01	0.80
			Age 8: vineyard	-4.29	1.73	-2.48	0.01
			Age 9: vineyard	-6.03	1.82	-3.32	0.002
Landing Accuracy	GLMM (Gaussian)	Square root	Intercept	1.46	0.14	10.57	<0.001
			Age 7	0.39	0.14	2.74	0.008
			Age 8	0.45	0.14	3.18	0.002
			Age 9	0.68	0.15	4.55	<0.001
Landing Difficulty	GLMM (Gaussian)	Square root	Intercept	1.48	0.11	13.46	<0.001
Proportion of flights that are chases	GLMM (binomial)	None	(Intercept	-8.12	1.22	-6.66	<0.001
			Age 7	2.08	0.64	3.23	0.001
			Age 8	2.05	0.62	3.32	<0.001
			Age 9	2.10	0.62	3.38	<0.001
			Siblings	4.02	0.96	4.21	<0.001
			Wild-reared	3.71	1.02	3.64	<0.001
			Age 7: wild-reared	-2.27	0.76	-3.01	0.003
			Age 8: wild-reared	-2.29	0.72	-3.16	0.002
			Age 9: wild-reared	-2.44	0.76	-3.21	0.001
Mean frequency of hunting attempts	GLMM (Gaussian)	Arcsin square-root	Intercept	0.03	0.02	1.30	0.19
			Wild-reared	0.03	0.02	1.48	0.19
			Siblings	0.12	0.05	2.65	0.01
			Wild-reared: Siblings	-0.16	0.05	-3.23	0.003

Separate generalised linear mixed models were run for each response variable and maximal models included the following predictors: age, rearing method (wild-reared with parents or released without parents), sibling presence, individual sex, and habitat type (vineyard or hill). Models were simplified based on AIC. The intercept represents the lowest values for all variables retained in the model, with age 6, released without parents, siblings absent, female, and hill habitat as the lowest values for each of the variables above, respectively. Individual sex was removed from all simplified models. Colons (:) between two terms represent an interaction effect within the model. The test statistic for all predictor variables represents a *t* value, except for un-penalised binomial models where a *Z* value is given. Estimates from the binomial models are from a logit-link function and to convert the estimates to true proportions the values need to be inverse-linked ($e^{\eta} / (1 + e^{\eta})$).

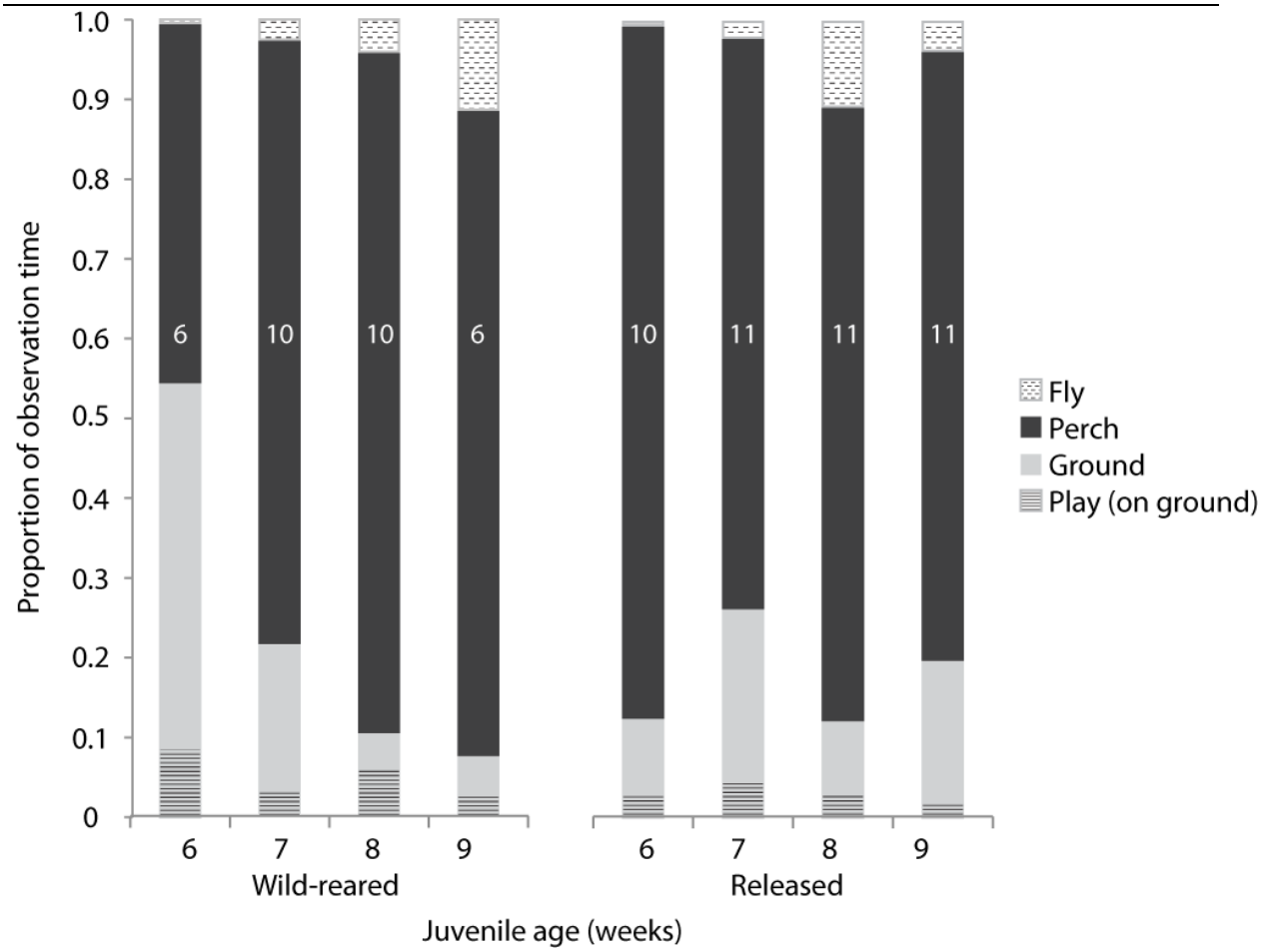

Figure 6.2. Mean proportion of observation time that juvenile falcons spent walking on the ground (*Ground*), perched off the ground (*Perch*), or flying (*Fly*). Playing (*Play*) generally took place on the ground so has been included as a component of time spent on the ground. Juveniles were either 'wild-reared' and therefore raised by adult falcon parents, or were 'released' and reared without parents after being released from an artificial nest site as part of a reintroduction programme. Numbers within each column represent sample sizes.

Age was also positively correlated with frequency of flights. At 6 weeks old, juveniles flew a mean of 0.08 ± 0.02 times per minute, and at 7 weeks old they flew 0.11 ± 0.02 times per minute, although this difference was not significant (t = 1.32, p_{MCMC} = 0.22; Fig. 6.4b). Compared to age 6 weeks, juveniles flew significantly more often in week 8 (0.21 ± 0.03 flights/min; t = 3.741, p_{MCMC} < 0.001; Fig. 6.4b) and in week 9 (0.219 ± 0.056; t = 3.94, p_{MCMC} < 0.001; Fig. 6.4b).

Mean *flight distance* was also positively affected by age, but this varied with habitat type. In weeks 6 and 7 there was no change in the mean flight distance (all t < 1.5, all p_{MCMC} >

0.15; Fig. 6.4a). In week 8 and then week 9, juveniles significantly increased their mean flight distances in both managed vineyard and unmanaged hill habitats (week 8: $t = 4.70$, $p_{MCMC} < 0.001$; week 9: $t = 6.76$, $p_{MCMC} < 0.001$; Fig. 6.4a), although this increase was less steep in vineyards (week 8: $t = -2.48$, $p_{MCMC} = 0.01$; week 9: $t = -3.32$, $p_{MCMC} = 0.002$; Fig. 6.4a). *Landing accuracy* was only influenced by juvenile age, with an increase in landing accuracy across each week (all $t > 2.7$, all $p_{MCMC} < 0.008$; Fig. 6.4c), but all other factors (sex, habitat type, presence of parents or siblings) were removed from the reduced model. Similarly, the *landing difficulty* did not change according to any of our variables, including age, and remained constant at 2.55 ± 0.06.

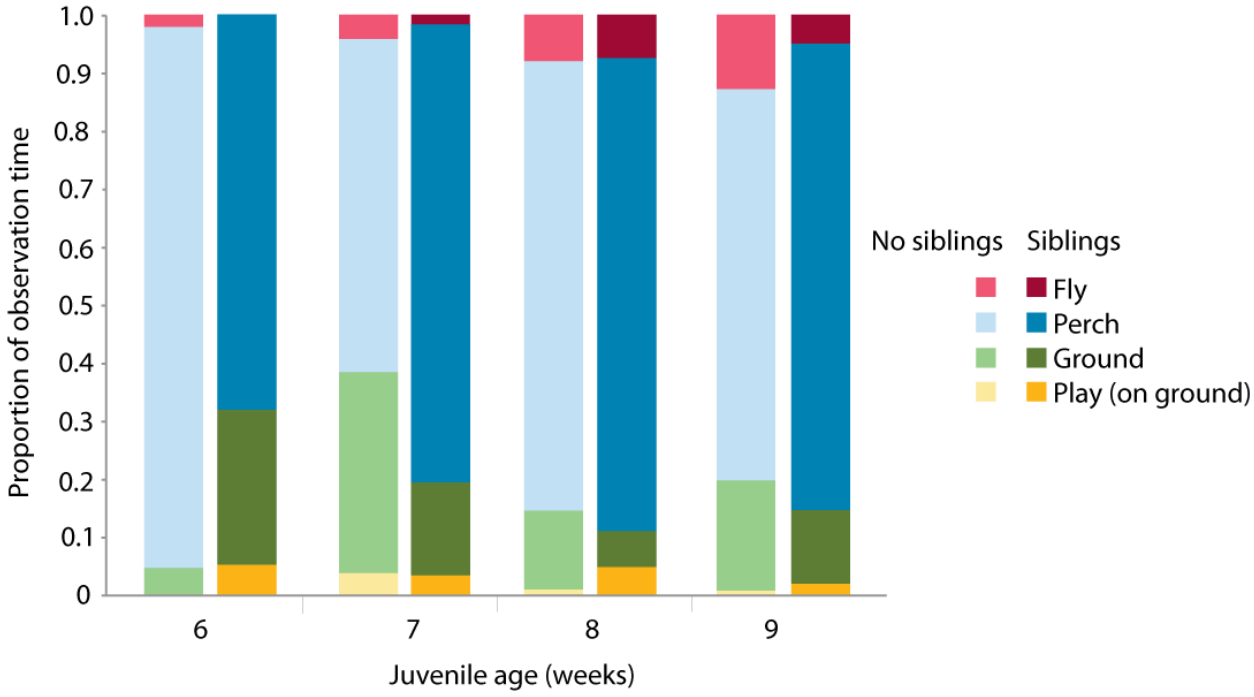

Figure 6.3. Mean proportion of observation time that juvenile falcons with siblings (darker shades) and juvenile falcons without siblings (lighter shades) spent walking on the ground (*Ground*), perched off the ground (*Perch*), or flying (*Fly*) in the four weeks following fledging or release. Playing (*Play*) generally took place on the ground so has been included as a component of time spent on the ground.

Holding all other variables constant, a greater proportion of the total flights were *chases* for birds that had siblings compared with single birds ($Z = 4.21$, $p < 0.001$) and for wild-reared juveniles compared to released juveniles ($Z = 3.64$, $p < 0.001$). The proportion of chase flights increased with age (all $Z > 3.2$, all $p < 0.002$). Model estimates indicated that over weeks 7, 8,

and 9 the slope for the relationship between age and proportion of flights that were chases decreased for wild-reared juveniles compared to released juveniles (all $Z > 3.00$, all $p < 0.003$), although the proportion of flights that were chases were still higher for wild-reared birds.

We observed 75 *hunting* attempts by juveniles, none of which were successful. Comparing juveniles with and without siblings or parents we found that wild-reared juveniles with siblings hunted the least (0.003 ± 0.001; $t = -3.23$, $p_{MCMC} = 0.002$); released individuals without siblings hunted slightly more often (0.005 ± 0.004; $t = 2.65$, $p_{MCMC} = 0.01$); released individuals with siblings had a non-significant tendency to hunt more often (0.009 ± 0.002; $t = 1.48$, $p = 0.08$); and wild-reared juveniles without siblings had a non-significant tendency to hunt the most often (0.023 ± 0.009; $t = 2.65$, $p = 0.21$). We observed 19 *food passes* between adult and juvenile falcons. While the accuracy of food passes seemed to improve with age, the sample size was too small to test for statistical analysis. In week 6, we only observed one food pass with an accuracy of 2; in week 7, we observed 2 food passes (mean accuracy 2.75 ± 0.75); in week 8 we observed 6 food passes (3.22 ± 0.58); and in week 9 we observed 3 food passes (4.33 ± 0.67).

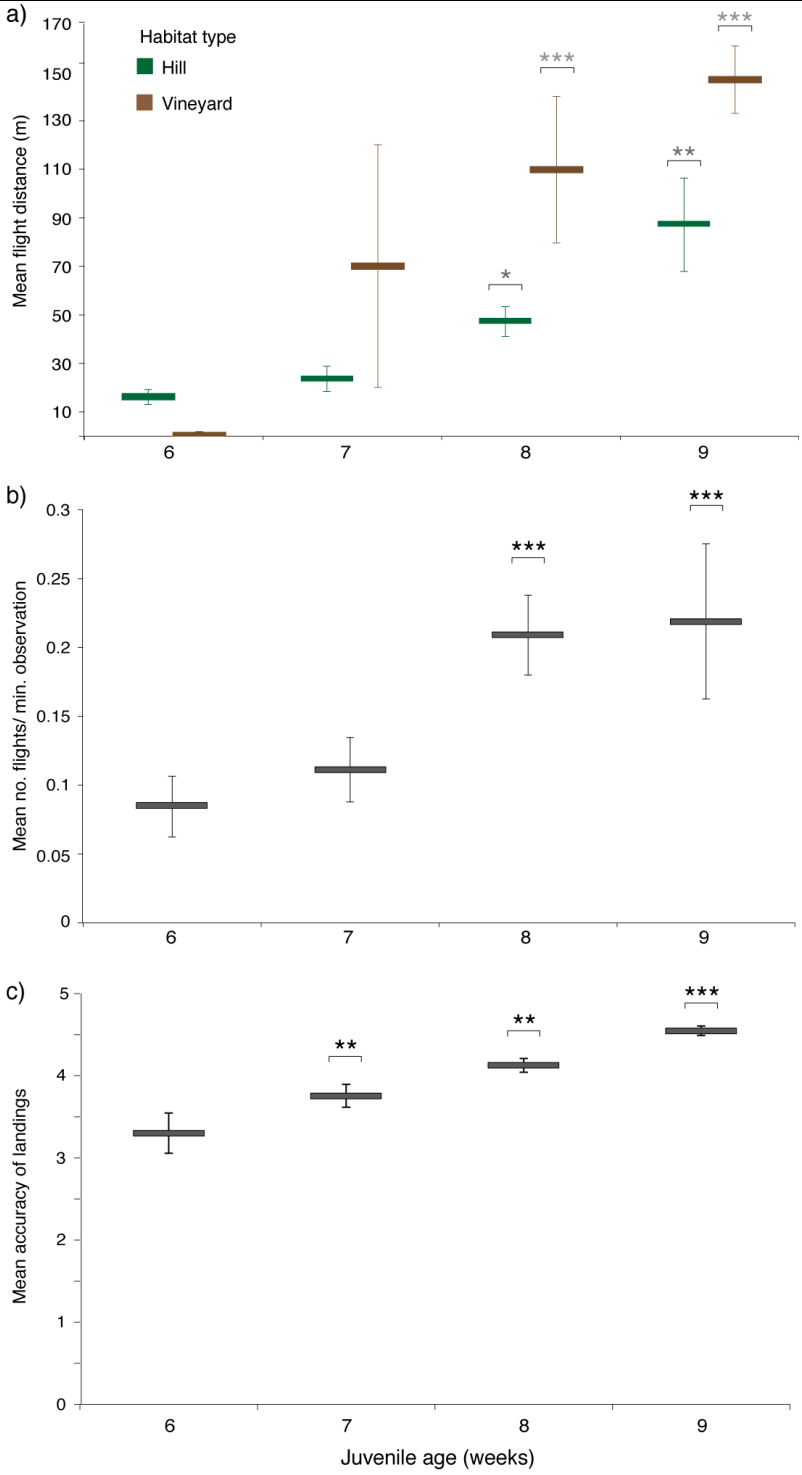

Figure 6.4. Effect of age (weeks) on the development of flight behaviour in juvenile New Zealand falcons (*Falco novaeseelandiae*) that were either wild reared with parents or released from artificial nests and reared in the absence of parents. Flight development was measured by a) the mean distance flown by juveniles per week; b) the mean number of flights observed per unit of observation (min); and c) the accuracy of landing attempts. Asterisks denote significant changes between each week and the baseline (week 6) according to the results of a generalised linear mixed model. *$p < 0.05$, **$p < 0.005$, ***$p < 0.0005$.

DISCUSSION

Solitary conditions in the early stages of development can have negative effects on social development (Lévy et al. 2003), hunting skills (Edwards 1989), and brain growth (Punzo & Ludwig 2002). While in some other birds of prey, individuals that have been released have been able to develop adequate hunting skills with little post-release contact with conspecifics (e.g., tawny owls, *Strix aluco*, Bennett & Routh 2000), our results support the notion that in the New Zealand falcon, where broods of 2 or 3 chicks are normal (Fox 1977), the presence of both parents and siblings is likely to result in the fastest development of important flight and foraging behaviours. Single chicks without parents appear to be worst-off in terms of their development of flight, hunting, and social behaviours, and were often observed for hours at a time simply sleeping on tree branches. Furthermore, two of the four falcons that were released as single chicks during this study were killed (one electrocuted, and one poisoned) within 4 months of being released.

Parents train young birds in hunting skills through the provisioning of food and through demonstrating hunting within view of their offspring (Newton 1979; Kitowski 2009). In *F. novaeseelandiae*, food passes from parents, chases of conspecifics, and play behaviour are all likely to provide experience needed for the hunting of prey later in life (Negro et al. 1996; Kitowski 2009). The combination of all of these behaviours should be taken into account when considering the behavioural development of juvenile falcons. We did not find any obvious trends in the frequency of hunting attempts and the conditions in which juveniles were raised. Our results suggest that wild-reared juveniles without siblings and released juveniles with siblings hunted more often than the other two groups. Although the reasons for this are not clear, these observations may be a consequence of birds attempting to hunt for themselves more often if they are not focussed on beating their sibling/s for food provided by parents.

The importance of sibling presence on the behavioural development of raptors is not well known. Juveniles of many species, including eagle owls (*Bubo bubo*; Penteriani et al. 2005; Delgado et al. 2009), osprey (Edwards 1989), golden eagles (*Aquila chrysaetos*; O'Toole et al. 1999) and American kestrels (*Falco sparverius*; Negro et al. 1996) stay close to one another in the early stages of the post-fledging dependency period and increase distance

between siblings as they approach independence. While this is sometimes considered in light of potential competition amongst broodmates, there may be evolutionary benefits to remaining nearer to siblings in the early stages of development. For example, socially-reared precocial birds retain better species-specific visual imprinting capabilities compared to individuals reared in solitary conditions (Lickliter et al. 1993). The few studies that have examined the importance of sibling presence on the development of hunting in raptors have shown that individuals with siblings develop this vital foraging behaviour faster than single individuals (Edwards 1989). We observed single juveniles often perching or standing on the ground for long lengths of time, and our results suggest that single juveniles flew less often than juveniles with siblings.

The presence of siblings also triggered more play behaviour in young New Zealand falcons. Play behaviour in birds is most commonly described in Psittacines and Corvids and is associated with increased cognitive capabilities and foraging innovation (Diamond & Bond 2003; Ricklefs 2004). In raptors, play behaviour is correlated with the skill each species requires to hunt their prey: in species that actively pursue prey, such as falcons, play is reported more often than in species that are food generalists or scavengers (Ricklefs 2004; Kitowski 2005). Therefore, increased incidence of play in juveniles with siblings is likely to have implications for hunting skills later in life. We observed more play behaviour in birds with siblings than we did in solitary birds, possibly because the presence of a playing sibling triggers imitative play behaviour, and in the case of hunting attempts, imitative hunting, among observing individuals (Negro et al. 1996).

The increasing ability of juvenile falcons to fly and forage with age was consistent with other raptors (e.g. Lawrence & Gay 1991; Kitowski 2005), passerines (e.g. Weathers & Sullivan 1989; Heinsohn 1991), and seabirds (e.g. Yoda et al. 2004). We noticed a marked increase in the number of flights, the distance of flights, and the amount of play over the four weeks of our observation period. Juvenile male aplomado falcons are reported to pursue prey at a younger age than juvenile females (Brown et al. 2006). However, we did not detect any differences between the sexes for any of the behaviours that we measured.

For animal reintroductions to succeed, it is important that the natural history and behaviour of the animal be incorporated into the development of conservation management plans and policy (Knight 2001; Blumstein & Fernández-Juricic 2004; Berger-Tal et al. 2011) as the ability of translocated individuals to display natural behaviour can influence the success of

reintroduction projects (Blumstein & Fernández-Juricic 2004). The need to assess the behavioural ramifications of translocation is particularly acute when animals are reintroduced into anthropogenic landscapes. Experience with natural conditions, including predators and prey, as well as social interactions with conspecifics are all important considerations for release programmes. Wild-reared individuals often display higher survival rates than released individuals (Brown et al. 2006; Aaltonen et al. 2009; Reid et al. 2010), but this trend can be mitigated by pre-release conditioning. For example, raising black-footed ferrets (*Mustela nigripes*), in outdoor pens resulted in higher survival rates than raising individuals in indoor cages (Biggins et al. 1998), and waiting for red kites (*Milvus milvus*) to develop flight skills before releasing them resulted in reduced electrocution compared to traditional hacking of younger birds (Murn & Hunt 2008). All of the released juveniles in this study were raised in similar pre-release conditions and were released using similar hacking methods at approximately the same age. Further research is needed into the optimal pre-release and release conditions in order to optimise the survival and recruitment of released individuals.

Our results support the notion that in New Zealand falcons, at least, interactions with conspecifics in the post-fledging dependency period leads to faster development of flight and hunting behaviours, and is likely to result in greater social development. Individuals that survive the first winter after release and go on to breed have been shown to provide their chicks with higher nest attendance rates, more food, and a similar diet compared to wild-reared falcons (Chapters 4 & 5), supporting the idea that released individuals can develop the hunting and social skills needed to reproduce successfully. Our results suggest that the presence of siblings augments behavioural development and should be a requirement of any future releases of this species.

ACKNOWLEDGEMENTS

I am grateful to my supervisor Ximena Nelson for helping to plan these experiments and for providing essential feedback and comments on the analysis and writing of this chapter. E. Soper, B. Halkett & J. Knott assisted with data collection. We thank D. Parsons and Nelson Forests Ltd., winegrowers of ARA, B. Feickert at Wainui vineyard, Yealands Estate vineyard,

Talleys farms, Dumgree Vineyard, Lions Back, and E. Rentoul at Wye Hills farm for access to land. L. Olley provided information on juvenile releases.

SUPPORTING INFORMATION

Supplementary Video 5 contains examples of play behaviour in juvenile falcons, as well as examples of food passes from adult falcons to juveniles. Be aware that these videos were shot with a hand-held camcorder and are therefore shaky at times.

CHAPTER SEVEN

NEW ZEALAND FALCON NESTS SUFFER LOWER PREDATION IN AGRICULTURAL HABITAT THAN IN NATURAL HABITAT

Vineyard habitat in Marlborough (Photo: S. Kross)

Kross, S.M., M^{c}Donald, P.G., & X.J. Nelson. Under Review. New Zealand falcon nests suffer lower predation in agricultural habitat than in natural habitat.

ABSTRACT

Agricultural lands are rarely the focus of conservation initiatives. However, these environments may be beneficial if reproductive parameters, such as predation rates of offspring, are lower in production landscapes than in remnant natural areas. Introduced mammalian predators have been implicated in the majority of avian extinctions on oceanic islands around the globe. Nowhere is this more apparent than in the decimated New Zealand avifauna, where introduced predators remain the primary threat to virtually all surviving endemic species, including the threatened New Zealand falcon (*Falco novaeseelandiae*). We used remote videography at falcon nests and conducted an artificial nest experiment to compare the rates of predation and responsible predators of falcons nesting in hills against those nesting in nearby commercial vineyards. Overall, 63% of artificial nests in the hills were predated, compared with 38% in vineyards. Further, artificial eggs were predated faster in the hills than those placed in vineyards. Video footage revealed that the suite of predators visiting real falcon nests was similar to those identified attacking artificial nests. However, predators differed across habitats, with nests in vineyards being predated mainly by hedgehogs (*Erinaceus europaeus*), and harriers (*Circus approximans*), whereas nests in the hill environments were mainly attacked by stoats (*Mustela erminea*). These results demonstrate the important implications of habitat type on predation pressure associated with introduced predators. These may well prove a fruitful avenue of management if breeding can be fostered in safer areas, as in the case of this threatened falcon.

INTRODUCTION

Habitat modification for agriculture is the leading cause of declines in avifauna worldwide (Green et al. 2005). Primary production regions globally continue to expand, while areas of native vegetation shrink (Foley et al. 2005). Despite this, conservation initiatives for threatened species rarely focus on areas of production, and instead hinge upon regions of remaining native vegetation. Reserves tend to be found in rugged and inaccessible areas of low economic value (Margules & Pressey 2000), whereas production lands tend to be accessible and to have a high availability of resources, both natural and supplemented. There have been calls to extend the conservation mind-set into our agricultural regions through the use of farming practices that are wildlife-friendly (Edwards & Abivardi 1998; MacLeod et al. 2008; Fisher et al. 2011). Similarly, encouraging wildlife to return to production landscapes can improve functional diversity and has the potential to provide ecosystem services such as pest control (Foley et al. 2005).

Pest control is critical because introduced predators can have a devastating effect on avian populations, particularly in areas where naïve prey may reside, such as on oceanic islands (Blackburn et al. 2004). For example, predation by feral cats (*Felis catus*) has contributed to over 9% of avian extinctions worldwide (Medina et al. 2011), while invasive rats (*Rattus* spp.) have been introduced to over 90% of the world's islands, where they have had a significant negative impact on over 170 plant and animal taxa, and have been associated with the decline or extinction of 60 vertebrate species (Towns et al. 2006). Similarly, hedgehogs (*Erinaceus europaeus*) have been implicated in the decline of breeding shorebirds on Scottish islands to which they have been introduced (Jackson et al. 2004). Nowhere is the detrimental impact of these introduced species more apparent than in New Zealand, where exotic mammals have been implicated in the decline of most of the 58 avian species that have become extinct since the arrival of humans, approximately 2000 years ago (Wilson 2004).

Mainland populations of New Zealand native species continue to face population declines due to predation by introduced mammals. The survival of many remaining endemic species is now contingent on their reintroduction to predator-free islands, a practice honed in New Zealand with considerable success (Wilson 2004). More recently, fenced 'mainland islands' - intensively managed predator-free areas of the large North and South islands - have

been successfully established in order to protect a more representative contingent of New Zealand's biodiversity (Saunders & Norton 2001). However, this requires large areas of suitable habitat to be used for conservation initiatives, and may have direct economic implications due to the unavailability of land for other uses, such as agriculture (Margules & Pressey 2000).

Given this conflict, methods aimed at reducing the impact of agricultural activities and increasing the biological value of land being utilised in this manner are being actively sought. One such project is the joint conservation- pest management programme called 'Falcons for Grapes' (FFG), initiated in 2005. Its aim is to establish a population of New Zealand falcons (*Falco novaeseelandiae*) in the vineyard-dominated valleys of the country's largest wine-growing region by relocating individual falcons from nearby hills into vineyards (MAF 2009b). It has already been demonstrated that falcons can provide economic gain for vineyards in the form of pest control (Chapter 2) and that compared with their counterparts in the hills, falcons living in vineyards exhibit higher attendance and feeding rates at their nests (Chapter 5). However, evaluating whether vineyards provide habitat in which predation rates are comparable or lower than that of the surrounding hills is critical in assessing the success of this reintroduction programme. This is especially important because in other parts of the world agricultural land has been associated with higher nest predation rates for birds (e.g., Bayne & Hobson 1997; Vander Hagen et al. 2002), frequently due to the introduced predators that are so prolific in New Zealand.

Typically a ground nesting species, the New Zealand falcon is the country's only remaining endemic bird of prey and this threatened species is suffering ongoing population declines (Gaze & Hutzler 2004; Miskelly et al. 2008). It has been assumed that introduced mammalian predators have contributed to these declines (Fox 1977; Seaton et al. 2009), although direct evidence for this is limited to a single observation of a feral cat killing a brood (Chapter 3; further details herein). All other previous studies have used field signs, such as tracks or patterns of feather removal, to attempt to identify the cause of nest failures, although this method is frequently considered unreliable (Pietz & Granfors 2000). Additionally, the assumption that predation is the cause of the disappearance of all eggs and chicks from nests likely overlooks non-predation events, such as egg breakage or nest abandonment, factors that may well have a significant impact upon avian populations (Ratcliff 1967).

While direct observations of predation events are the best method to obtain conclusive data on predation levels, the resources required to test a sufficient number of nests, particularly for a widely and patchily distributed predator such as the New Zealand falcon, is unfeasible. Low densities coupled with large home ranges in difficult terrain make it hard to locate falcon nests, especially while they are still in the incubation stage (Lawrence 2002). Further, as with many raptor species, pairs that suffer early nest failure often go undetected (Newton 1979). Nests with young become easier to detect over time because of increased activity at the nest, audible calls from chicks, and conspicuous faecal build-up (Steenhof & Newton 2007).

As approximations of true avian nests, artificial nests provide an opportunity for scientists to manipulate conditions to better understand the factors influencing nest predation (e.g., Wilson, G. et al. 1998; Lewis et al. 2009; M^{c}Donald et al. 2009) and have been used to determine the animals responsible for egg predation in over 300 studies of avian species worldwide (Moore & Robinson 2004). Artificial nests are attractive to researchers, particularly for the study of threatened species, because they do not involve manipulation of natural nests and can reach sample sizes that are normally difficult to obtain, and also because the biases associated with finding natural nests can be controlled for (Major & Kendall 1996; Lewis et al. 2009; M^{c}Donald et al. 2009). However, it is important to recognize the limitations of this method for drawing inferences (Major & Kendall 1996), as artificial nests may not accurately mirror natural predation rates (Wilson, G. et al. 1998; Berry & Lill 2003; M^{c}Donald et al. 2009).

The success of the FFG project lies in the long-term ability of falcons to breed and live within the vineyard landscape. If nest predation rates are the same as, or higher, in vineyards than in the unmanaged land in the surrounding hills it may; a) explain why so few falcons are naturally seen in vineyards despite an abundance of prey; and b) provide evidence with which to inform a predator control scheme in vineyards that could alleviate this problem and potentially open up additional habitat for this species. Alternatively, if predation is lower in vineyards it may support the notion that the reintroduction of falcons into this intensive agricultural habitat is beneficial for ongoing conservation efforts for this and other species.

METHODS

Study area and species

Our study was based in Marlborough, the northeastern province of New Zealand's South island (41.52°S, 173.872°E). The region is mainly arid, with a monthly rainfall of 45.4 to 71.6 mm between October and February. The landscape consists of river valleys dominated by intensively managed viticulture, and unmanaged rugged hills covered by a mix of native and introduced grasses and native shrubs (see Chapter 3 for details). *F. novaeseelandiae* is a sexually dimorphic species, with females in our study area weighing an average of 531g and males weighing 330g (Fox 1977). The breeding season ranges from September to February, with most egg-laying occurring in October and November and an incubation period of four weeks, after which parents raise chicks for 30-35 days before they fledge (Fox 1977). During this time, falcons are territorial within their estimated 3.8 km^2 home range and are highly aggressive towards intruders near their nests (Fox 1977).

Artificial nest experiment

Yellow microcrystalline wax (Conservation Supplies, Warkworth, NZ) was poured into plaster moulds that had been created from real falcon eggs. We used wax eggs to avoid the problems of having egg shells that were too thick for some predators to pierce (Major & Kendal 1996), of natural eggs becoming rotten when left out in the field, and to avoid creating a positive experience (i.e., a food reward) that could be associated with a nest that smells and looks similar to the nests of our threatened study species. Microcrystalline wax was used because it is relatively scent-free, and because it has a high melting point (80°C) and therefore does not melt in the field. A looped metal wire was inserted into each egg as it was moulded to act as an anchor for pegging eggs to the ground. Eggs were aired outside for two weeks after moulding and then were painted light brown using waterproof exterior house paint ('desert sand', Resene Paints, Lower Hutt, NZ). This provided better resolution of any bite marks, and approximated natural falcon egg colouration, at least from a human perspective. Previous studies have shown that the colour of eggs is unlikely to affect predation rates (Major & Kendal 1996), and typical mammalian predators of falcon nests are unlikely to use visual cues as the primary nest

detection source (M^{c}Donald et al. 2009). Once painted, eggs were aired outside for a further two weeks to ensure that they had a neutral scent prior to being used for this experiment.

Substrate samples were then taken from within and immediately around the nest of a pair of captive New Zealand falcons and all of the wax eggs were placed in a box containing this material for between two-three weeks prior to their use. Additional nest substrate was collected from a natural falcon nest and a handful of this was placed under all eggs when they were deployed.

Nineteen artificial nests were deployed in unmanaged hill habitat ('hill nests') and 21 artificial nests were deployed in managed vineyard habitat ('vineyard nests'). Nest sites were chosen that were a minimum of 4 km apart, this being the mean distance between falcon nests in Marlborough (Fox 1977) and also similar to the home range of stoats, *Mustela erminea*, in New Zealand (Smith et al. 2008). Nests were made by creating a shallow (2 cm) depression in the ground and lining it with nest substrate (see above) to mimic a real nest. A metal peg, completely inserted into the ground and covered with soil and nest substrate, was used to attach two artificial eggs to the ground to ensure that they could not be removed by predators. Falcons in our study area normally nest under boulders or fallen trees (Fox 1977), but also nest at the base of trees (SMK, unpublished data). To minimise variance between sites, we placed all artificial nests at the base of trees. Maps and detailed descriptions of each site were used to relocate nests instead of markers, because markers may attract or repel predators (Major & Kendal 1996).

Artificial nests were set out between 15 and 30 November 2010, alternating between placements of sets of vineyard and hill nests. All nests were checked two weeks after being deployed (recalling that incubation for this species lasts 30 days), and if predation was found to have occurred the nest was removed. We checked nests again after four weeks. All eggs were examined by hand, and nests were considered to have been predated if tooth or beak marks were visible on either of the eggs. If present, these marks were easily visible because if the thin paint layer was scratched the yellow wax underneath was readily apparent. All predated eggs were compared to a skull collection at the national Te Papa museum in Wellington, which included potential avian and mammalian predators found in the study area.

Remote videography

We used remote videography to monitor six nests in the unmanaged hill areas and five nests in vineyards over three breeding seasons (October 2008- January 2011). The systems worked on a motion-detection threshold, and recorded at 30 fps. Recordings were in colour during the day, and used near-infrared lighting for black-and-white recordings during darkness (see Chapter 3 for details). Falcons breeding in the vineyards had their nests moved into artificial 'nest barrels', consisting of 60 x 110 cm plastic drums cut with a 55 x 30 cm opening. These were raised from the ground by the FFG team following hatching to protect chicks from potential predators. For these nests, cameras were placed either immediately outside of the nest barrel on a wooden post (n = 2), or were mounted to the inside of the barrel itself (n = 4). In both cases, the cameras could record behaviour inside of the barrel and in the area immediately in front of the barrel. For all ground nests, cameras were placed between 0.5 and 1 m from the nest scrape on the ground, and were able to capture all behaviour within the scrape and immediately adjacent to it. In all cases where an animal came into view near the nest scrape, video was viewed frame-by-frame in order to identify the animal and to analyse its behaviour.

RESULTS

Artificial nest experiment

In total, 12 out of 19 hill nests were predated (63.2%) while 8 out of 21 (38.1%) vineyard nests were predated (Fig. 7.1). Despite the higher overall predation rates among hill sites, there was no statistically significant difference between the two habitats ($\chi^2 = 2.51$, $p = 0.11$). However, when comparing the predation rates for the first two weeks of placing artificial nests, there was significantly higher predation in hill nests (8 of 19 nests: 42.1%) than in vineyard nests (3 of 21 nests: 14.3%; $\chi^2 = 3.87$, $p < 0.05$).

Predators responsible for marking eggs differed significantly between the two habitats, with stoats attacking 7 of 19 nests in the hills, but none of the 21 nests placed within vineyards ($p = 0.003$, 2-tailed Fisher exact test). Other predator rates did not differ between habitats (Fig. 7.1). Hedgehogs attacked artificial nests at similar rates in the two habitats (5 nests in the hills and 4 nests in the vineyards, $p = 0.712$, 2-tailed Fisher exact test), as did Australasian harriers *Circus approximans* (1 nest in each habitat), Norway rats *Rattus norvegicus* (1 nest in the

vineyards, 0 hill nests), and ferrets *Mustela putoris* (1 nest in the vineyards, 0 hill nests; all 3 predators $p = 1.0$, 2-tailed Fisher exact test; Fig. 7.1).

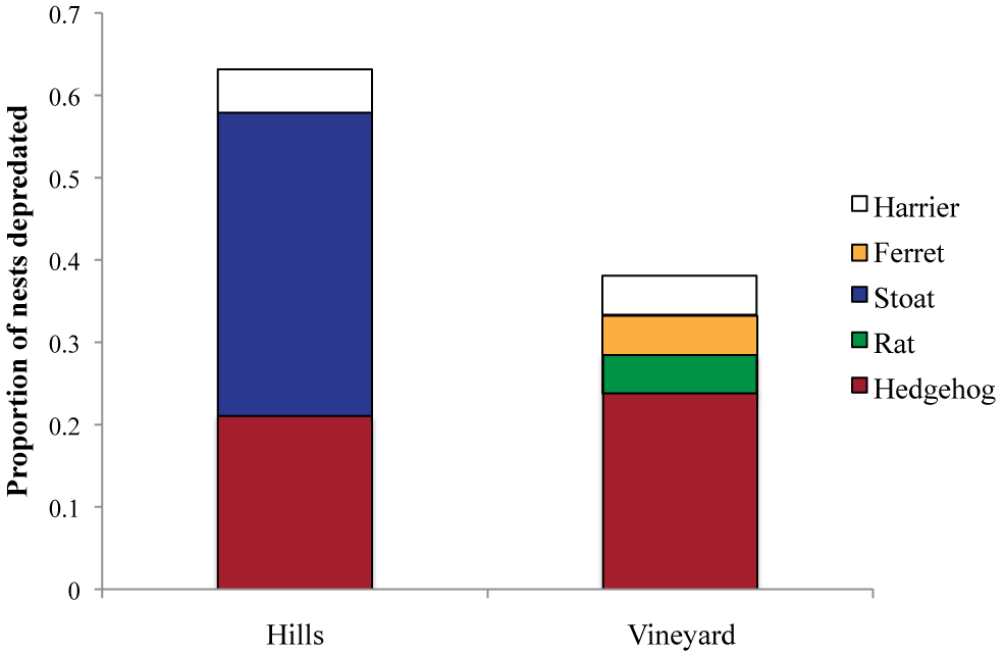

Figure 7.1. Proportion of artificial New Zealand falcon (*Falco novaeseelandiae*) nests in unmanaged hill habitat versus managed vineyard habitat predated by hedgehogs (*Erinaceus europaeus*), stoats (*Mustela erminea*), ferrets (*Mustela putoris*), Norway rats (*Rattus norvegicus*), and harriers (*Circus approximans*).

Remote videography

Potential predators were recorded at only one of the five vineyard nests. At this nest, our camera revealed a visit by a hedgehog (Fig. 7.2a) that the adult female seemed to be unaware of while brooding her young chick. We also recorded an attack by an Australasian harrier (Fig. 7.2b), the only indigenous predator detected in the entire study, that flew past the face of the nest barrel twice and attempted to grab the adult female falcon with its talons before being pursued by the female falcon. A little owl (*Athene noctua*; Fig. 7.2c) was also observed landing within the nest barrel before turning around quickly and attempting to fly away. The adult female, who was inside the nest barrel at the time but may not have been visible from outside of the barrel, attacked and appeared to capture the owl. Little owls have been recorded in the diet of falcons in our study area (Chapter 4).

At hill nests, a number of non-predation events were recorded - all during nocturnal hours and all by introduced species. Three of these events were recorded at one nest. First, a red deer (*Cervus elaphus*; Fig. 7.2e) was observed entering the scrape and appeared to be chased away by the adult female after sniffing at the chick for approximately 10 s. Two nights later, an unidentified species of rat (Fig 7.2d) was observed at the edge of the scrape for approximately 20 s but appeared to be deterred by the presence of the female falcon that reacted aggressively and adopted a defensive posture (raised body feathers, weight back, talons ready to strike; Fox 1977). Finally, a stoat attacked a 35-day old female falcon chick (Fig. 7.2f). The chick survived the attack when the stoat (which was hanging onto the chick's rump) dropped off as the chick flew away. The young falcon was observed again being attacked by a stoat in daylight two weeks after fledging. She reacting by performing 'mock attack' play behaviour (often observed between juvenile falcons; Fox 1977) by flying past the stoat, striking it briefly with her talons, and then perching on a nearby rock. The stoat then attempted another attack and the falcon flew away unharmed.

A common brushtail possum (*Trichosurus vulpecula*) was observed on two separate occasions at a different hill nest. On the first occasion a possum entered the nest during the incubating phase and did not attempt to eat any of the three eggs, despite being within the scrape for over six min. The possum was then attacked by the adult female before running away (Fig. 7.2g). On the second occasion, a different possum (based on size and colour) entered the nest scrape the night after the chicks fledged and cleared away some food scraps before leaving.

A single successful predation event was recorded at a wild nest, when a feral cat (Fig. 7.2h) attacked and killed all three chicks over the course of two separate visits. One chick was presumably killed offscreen after the cat walked in front of the camera on December 15, 2008 and the chick wasn't seen again. Footage of the other two chicks, that were approximately 28-days old, being killed and eaten on the second of the two visits was obtained two days later, with some interesting behaviours observed. One chick was attacked immediately and the remaining chick stood next to the cat, visibly kekking (a territorial and alarm call) for almost two minutes, as the cat killed and began eating the first chick. During this time the adult female falcon entered the nest twice, walking in with wings spread, and attacked the cat with her talons. Two minutes later, the second chick moved away from the cat, walking out of the view of the camera. The cat remained within the scrape and ate the first chick, then appeared to go to sleep.

Just under 2 h later, the cat was observed stalking past the camera and three min later pulled the remaining chick back into the nest scrape. The chick was grasping a rock and a large amount of loose foliage in its talons. This nest was located on a small, approximately 3 m in diameter, ledge on a low cliff, so had the chick moved more than three metres from the nest scrape it would be unlikely that the cat would have pulled it back into the nest to kill it. This leads us to believe that the remaining chick hid underneath a nearby shrub for over 100 min between the first attack and the final fatal encounter.

In addition to the predation footage, one camera at a vineyard nest recorded a female falcon breaking her own eggs and subsequently eating them. This footage provided important evidence that predators are not always responsible for nest failures, even when eggs disappear or eggshells are found at a nest.

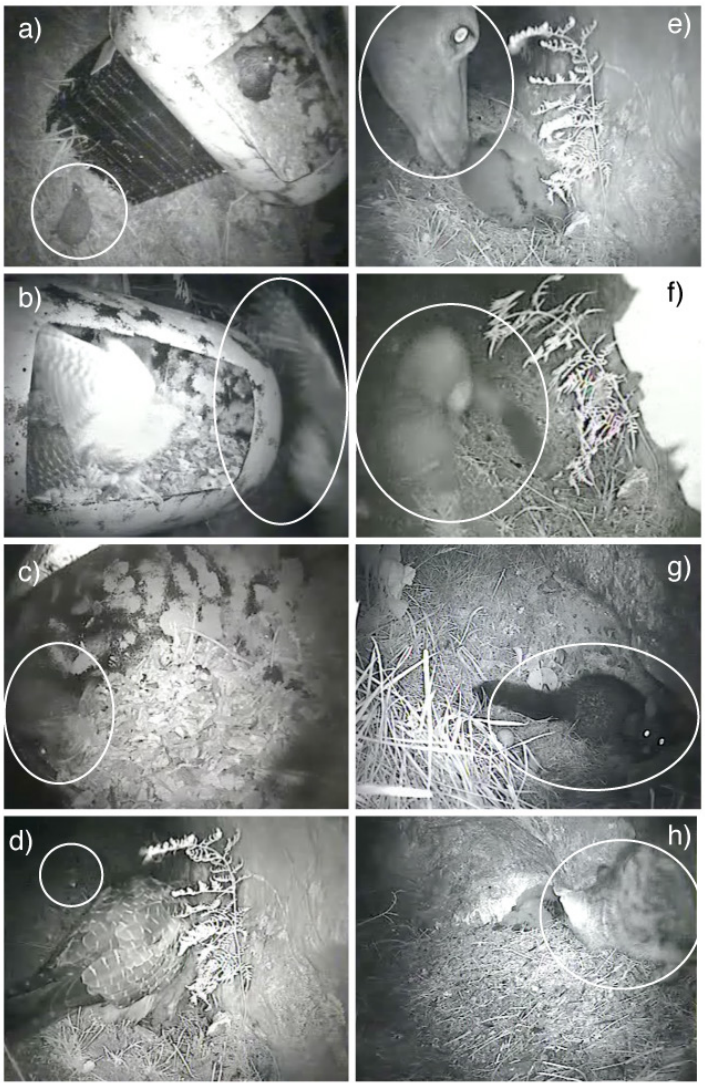

Figure 7.2. Still shots of predators from video cameras set up at New Zealand falcon nests in vineyard habitat (a-c) and unmanaged hill habitat (d-h). All three vineyard images were from the same nest which had been lifted off of the ground in an artificial barrel. Predators included: a) a hedgehog (*Erinaceus europaeus*); b) an Australasian harrier (*Circus approximans*; wing and spread tail are visible); c) a little owl (*Athene noctua*; eye is visible and wing appears as a grey blur); d) a rat (*Rattus* spp.; eye is visible as white spot, species is unknown); e) a red deer (*Cervus elaphus*); f) a stoat (*Mustela erminea*); g) a brushtail possum (*Trichosurus vulpecula*); and h) a feral cat (*Felis catus*). Only the feral cat successfully predated a nest; killing all 3-chicks. The deer, stoat and rat were all observed at a single hill nest. Video clips from all of these events are included in Supplementary Video 6.

DISCUSSION

The results of our experiment showed that artificial nests in the hills were predated faster and more often than those in the vineyards. This has important implications for conservation, as our findings support the notion that in some cases production landscapes can be beneficial habitat for the recovery threatened species. Thus far, most studies comparing nest predation in

agricultural and natural settings have been focused on continental datasets. Our study offers evidence that on an island, where introduced mammals are the main cause of species declines, production land may offer a comparatively safe refuge from primarily introduced predators.

The footage from our remote videography systems provided evidence that the same predators we detected in our artificial nest experiment also targeted real falcon nests, but that actual predation events were lower for the natural nests, as has been suggested by previous artificial nest experiments (Wilson, G. et al. 1998; Berry & Lill 2003). In this study, the video system used enables parental defence of the nest site to be clearly implicated as the most likely factor behind this difference, although the interaction with the feral cat also demonstrates that not all predators can be rebuffed. All of the nest predators observed visited nests at night, as has been found in other studies of nest predation in New Zealand (Sanders & Maloney 2002).

Our footage of the female falcon breaking, and then eating, her own eggs provided important evidence that predators are not always responsible for nest failures, even when eggs disappear or eggshells are found at a nest. Prior to this footage being obtained, missing falcon eggs were generally presumed to have been predated. The cause behind this behaviour is unknown, but could be due to a drop in body condition of the female that made breeding unsustainable, or due to high levels of disturbance from vineyard or FFG activities. Nevertheless, our footage also revealed that nest predation is likely a significant contributor to the decline of this species.

Hedgehogs were the main predator that attacked our artificial nests in the vineyards, and the second most important predator of eggs in the hills. Since their purposeful release by acclimatisation societies in the late 1800's and early 1900s, hedgehogs have become common throughout New Zealand, particularly in the low-lying agricultural regions, but extending into alpine zones (Brockie, 1975; Wilson, 2004). Hedgehogs have been shown to feed on the eggs of ground-nesting avian species, including the critically endangered black stilt (*Himantopus novaezelandiae*) and black-fronted tern (*Sterna albostriata*; Sanders & Maloney 2002), along with a number of threatened reptiles and invertebrates (Jones et al. 2005). In contrast, stoats were the major predator that visited artificial nests placed in the hills. *Mustela* species were deliberately released in New Zealand in the late 19th and early 20th centuries as a biocontrol for rabbits, (*Oryctolagus cuniculus*). However, as particularly voracious predators, stoats have since been implicated in the population declines of many native birds, including blue duck

(*Hymenolaimus malacorhynchos*; Whitehead et al., 2008), several kiwi (*Apteryx* spp.; McLennan et al. 1996), Hutton's shearwaters (*Puffinus huttoni*; Cuthbert 2003) and the kaka (*Nestor maridionalis*; Wilson, P. et al. 1998). Our video footage revealed that aside from feral cats, stoats were the only predators that attacked fully-grown falcon chicks. With the additional knowledge gained from impressions left by stoat teeth in our artificial nests, our data suggest that these mustelids may be one of the most dangerous predators for falcons, as they appear to target offspring throughout the entire breeding cycle from eggs through to independence. Cats are also particularly dangerous, as they target not only chicks, but also adult birds (Sanders & Maloney 2002).

Our observations of predation and near-predation events provide evidence that falcon chicks lack viable antipredator behaviours when faced with mammalian predators. In the case of the feral cat, the final chick to be killed appeared to react to the presence of this predator by hiding within 3 m of the cat. Similarly, we observed a juvenile falcon seemingly 'playing' with a stoat only weeks after being attacked by the same type of predator. Even when researchers visit falcon nests, chicks tend to remain completely still, and even let themselves be handled without attempting to escape (Fox, 1977; SMK, personal observation).

Nevertheless, our results suggest that it is likely that the primarily herbivorous mammals that we detected (deer and brushtail possum) are only a rare source of danger for falcons and may be deterred by the presence of adult birds, despite being a threat to birds in other regions (Pietz & Granfors 2000) and to other species within New Zealand (Wilson 2004). Additionally, it is evident that falcons are particularly aggressive toward avian predators such as harriers and owls (Fox 1977), both of which were recorded at nests in this study (Fig. 7.2b,c), and it is likely that the presence of adult falcons at nests serves as sufficient protection from these predators. The New Zealand avifauna, including falcons, evolved with birds of prey as their main predators (Wilson 2004), and this may explain why falcons display rigorous antipredator behaviour towards other birds but rarely towards mammals.

Experiments using artificial nests can help to predict the types of predators that are likely to target real nests (Moore & Robinson 2004; Lewis et al. 2009), and our additional direct observations of predators at real falcon nests provides substance to those predictions. However, while we did not detect any influence of our camera systems on the behaviour of falcons or their predators (Chapter 3), remote videography systems may attract or deter certain predator species,

despite not being externally visible, and may subtly change the behaviour of the subjects (M^{c}Donald et al., 2007). Therefore, these findings should not be relied on to accurately predict actual nest predation rates for New Zealand falcons. These findings do elucidate that there are differences of potentially lethal predators in these different habitats. While hedgehogs and birds were found to predate nests in vineyard sites as frequently as they did in the unmanaged hills, these species are more likely to be deterred by adult falcons than feral cats or than the predominant species detected in the hills, stoats.

As found around the world (Margules & Pressey 2000), most conservation initiatives in New Zealand focus on remaining tracts of native vegetation, despite almost 60% of the nation's land area being used for production (MacLeod et al. 2008). Globally, primary production regions are expanding, while areas of native vegetation continue to shrink, highlighting the need to extend the conservation initiatives into agricultural regions where feasible (Edwards & Abivardi 1998; Fischer et al. 2011). In some cases, conservation may also benefit agriculture through provisioning of ecosystem services, such as pest control (Chapter 2). Uniquely, we found that predation rates were likely to be lower in an agricultural setting, which is contrary to findings from overseas studies (Bayne & Hobson 1997; Vander Hagen et al. 2002). This highlights the importance of species-specific assessment of habitat quality. Coupled with previous results indicating that falcons living in vineyards demonstrate higher nest attendance rates and provide more food to their chicks (Chapter 5), this suggests that vineyards hold considerable potential for the conservation of New Zealand falcons, and further supports the notion that, pending assessment of their suitability, primary production systems could be used for conservation initiatives of this and similar species.

ACKNOWLEDGEMENTS

I'd like to thank Paul M^{c}Donald who assisted with the planning of this experiment and commented on the manuscript. Ximena Nelson helped with planning, analysis, and also provided comments on the manuscript. We thank all of the landowners who gave us access. P. Gaze & P. Bradfield from DoC provided helpful advice, as did D. Smith, and G. Stone at Te Papa. N. Hyde at Wingspan Bird of Prey Trust assisted with ferret skull identification, and L. Young identified the red deer. R. Brackley assisted with artificial nest placement, and a large

number of volunteers assisted with remote videography placement. L. Olley gave access to captive falcons.

SUPPORTING INFORMATION

Supplementary Video 6 includes video clips of the still shots shown in Figure 7.2.

CHAPTER EIGHT

DISCUSSION

Autumn vineyard and female falcon (Photo: S. Kross)

DISCUSSION

The expansion and intensification of agriculture is driving global biodiversity losses (Sala et al. 2000; Geiger et al. 2010), despite the fact that maintaining functional diversity within agricultural regions is essential for sustaining the ecosystem services upon which humans rely (Costanza et al. 1997; Daily et al. 2000; Tilman et al. 2002; Diaz et al. 2006; Perrings et al. 2006). With the growing footprint of agriculture, and the inability of shrinking areas of natural habitat to protect all threatened species, conservation initiatives are being encouraged to refocus upon agricultural landscapes (Edwards & Abivardi 1998; MacLeod et al. 2008). Reintroductions of threatened predators may be a potential way to increase the range of these species while concomitantly providing agricultural regions with a natural form of pest control. However, the success of reintroduction schemes hinge upon the survival of the species concerned, which in turn depends on the species' ability to perform necessary behaviours (Blumstein & Fernández-Juricic 2004) and to have access to necessary resources, such as food and shelter (Fisher & Lindenmayer 2000; Armstrong & Seddon 2008). On the other hand, if a species is able to survive- or even thrive- in an agricultural region, it may not provide ecosystem services at a level that is financially viable.

This thesis provides novel evidence for a mutually beneficial relationship between the conservation of a threatened predator and agriculture. I have shown that falcon presence in vineyards reduces the abundance of pest birds, as well as reducing the damage caused to grapes by those birds, saving vineyards between US $234 and $326 per hectare (Chapter 2). I have also shown that falcons commonly prey upon species that are not considered pests in a vineyard landscape, such as house sparrows (*Passer domesticus*) and greenfinches (*Carduelis chloris;* Chapter 4), but that are considered pests in arable agriculture (Coleman & Spurr 2001). Therefore, biological control by New Zealand falcons is not limited to the vineyard landscape, and other farming systems could benefit from reintroducing this rare endemic raptor into their regions.

When predators are present within a system, they affect their prey not only through direct predation, but also through altering the antipredator behaviours of their prey (Brown et al. 1999; Laundré et al. 2001). Antipredator behaviours can change the foraging choices made by prey species (Suhonen 1993; Fernández-Juricic & Tellería 2000; Devereux et al. 2005; Newey 2007) and can have long-term implications for individual fitness and population dynamics

(Downes 2001). These behavioural changes can also have flow-on effects at lower trophic levels and impact greater ecosystem functioning as a whole. The presence of predators is therefore thought to create a 'landscape of fear' for their prey (Laundré et al. 2001). For example, reintroducing wolves (*Canis lupus*) into Yellowstone National Park U.S.A. resulted in an increase in vigilance behaviour in elk (*Cervus elaphus*) and bison (*Bison bison*), which in turn increased willow stand growth and songbird diversity (Ripple 2004; Gross 2008).

Falcons in agricultural landscapes in New Zealand also offer the possibility to test the effects of predator presence on avian species (Brown et al. 1988a, b; Brown et al. 1999a, b; Laundré et al. 2001; Kotler et al. 2002) in a field-based setting. Falcons have been extirpated from many agricultural areas of the country, so experimental reintroductions, bookended by before-and-after studies of the foraging behaviour of target pest species, could test the theories of how predator presence changes the behaviour of prey species. There is evidence that falcon presence does alter the foraging behaviour of some birds. For example, in Chapter 2, I showed that the presence of falcons in vineyards did not alter the abundance of the grape-pecking silvereye (*Zosterops lateralis*), but that falcon presence did significantly reduce the damage caused by silvereyes. The most likely explanation for this is a behavioural change in the silvereyes triggered by an increased perception of predation risk because of the presence of falcons. Importantly, a valuable opportunity to investigate the role of falcons on ecosystem functioning would be lost if falcons were to be reintroduced into a new region without first establishing baseline data and ongoing monitoring of the pre-existing fauna.

During the breeding season, parent birds must feed their growing offspring large amounts of food and this can result in large impacts on the prey of each species (e.g., Holmes et al. 1979). Many passerine species rely on feeding protein-rich insects to their young, even if the bird species itself is not insectivorous throughout the rest of its lifetime. Raptors feed their young the same prey that they will eat throughout their lives, mainly small vertebrates such as birds and rodents. I found that during the nestling-rearing period, New Zealand falcons fed their chicks a mean of 11.36 ± 0.27 prey items per day (both habitats combined, supplementary food included, Chapter 4). Across the roughly 35-day rearing period for falcon nestlings (Fox 1977), this would equate to approximately 398 prey items, 98% of which would be avian prey (Chapter 4). Even considering this relatively short period in the annual cycle, a pair of breeding falcons are clearly capable of consuming large numbers of prey. As a thought experiment,

assuming that parents feed their fledged offspring at a similar rate for the four weeks after fledging, and that each adult falcon consumes an average of 2 prey items per day throughout the remainder of the year, it is likely that one pair of falcons and their offspring consume 1,386 total prey items per year. This, paired with creating a landscape of fear for pests, has a flow-on effect on the amount of damage to crops.

Chapters 4, 5, and 7 showed that not only can falcons survive in an intensive vineyard landscape, but that they are better parents, eat a similar diet, and probably have lower nest predation rates than their counterparts in the unmanaged hills. Additionally, Chapter 6 showed that as long as juvenile falcons are released along with siblings, they are able to develop flight and hunting behaviours at a similar speed to wild-reared juveniles. While these results suggest considerable potential for conservation of falcons within agricultural systems, further research is needed in three key areas which are discussed in detail below: (1) optimal pre- and post-release methodology for increasing juvenile survival; (2) investigation into the potentially harmful effects of residing in an agricultural landscape, such as increased exposure to chemical pesticides and power lines (Appendix 2); and, (3) further research into the abundance of introduced predators in agricultural regions.

1. Reintroducing a threatened raptor into intensively managed anthropogenic habitats has the potential to open up new regions for conservation, but requires the science to back it up. The best pre- and post- release methods for releasing juvenile birds into these new habitats need to be developed. Considerable knowledge has been acquired through reintroduction projects for raptors overseas, but many use the same 'hacking' method used by the Falcons for Grapes project, which involves releasing young birds from an artificial nest around the time that they would normally fledge from natural nests (Sherrod 1983). Chapter 6 shows that released juvenile falcons are capable of developing flight and hunting behaviours as quickly (in some cases more quickly), than their wild-raised counterparts. This research shows that juvenile falcons rely on interactions with conspecifics for their development, and therefore should always be released in pairs or groups.

Despite evidence that nest predation rates are likely to be lower in vineyards (Chapter 7), predation is still likely to be one of the main limiting factors for falcon population growth. There is evidence that pre-release conditioning can be used to teach predator recognition to

other bird species (McLean et al. 1999), and this would be worth pursuing for juvenile falcons bound for release. Similarly, red kites (*Milvus milvus*) released at an older age have been shown to suffer reduced rates of electrocution compared with those released at an earlier age with more traditional hacking methods (Murn & Hunt 2008).

With increasing sample sizes and research questions defined *a priori*, it will be possible to test the efficacy of pre-release conditioning and delayed releases on individual survival. It will be also be possible to track whether cohort size or individual sex has an impact on release success, as has shown to be the case for peregrine falcons (*Falco peregrinus*; Dzialak et al. 2006).

2. It was outside of the scope of this study to undertake analysis of falcon eggshells or muscle tissue, but in a country dominated by agriculture such as New Zealand, even falcons nesting outside of agricultural habitat are likely to be exposed to agricultural chemicals through their environment or their prey. Investigating the potential impact of chemical toxicity in *F. novaeseelandiae* should be a goal of future research in order to determine if it may play a role in suppressing population growth or even in decreasing populations around the country.

The widespread use of organochlorine compounds such as DDT starting in the 1940s caused population declines of a number of bird- and fish-eating birds of prey including the peregrine falcon (Ratcliff 1967). DDT residues have been found to have caused eggshell thinning in a number of Australasian raptors (Olsen et al. 1993), including the New Zealand falcon (Fox & Lock 1978), although population declines were not attributed to the eggshell thinning. Nevertheless, with an already reduced population of New Zealand falcons suffering predation by introduced predators (Chapter 7) and being electrocuted by dangerous electro-utility structures (Appendix 2; Fox & Wynn 2010), any negative effects of pesticides on breeding success could have a significant impact on population growth or decline. Furthermore, many of the chemical compounds identified to cause mortality in raptors around the world are persistent in the environment and are bioaccumulative and biomagnified. Furthermore, these can be transported around the globe through the atmosphere with migratory species and on water currents (Henny & Elliott 2007), and could therefore pose a threat to New Zealand falcons even if the compounds themselves are not used in New Zealand.

Chemicals used to treat livestock or to poison vertebrate pests such as mice may also play a relatively unnoticed role in falcon mortality. Secondary poisoning of raptors through anticoagulant rodenticide compounds is common, particularly in owls and scavenging species (Henny & Elliott 2007). Fortunately, falcons rarely scavenge dead animals for food, so their exposure to dangerous compounds such as lead shot and secondary poisoning through anticoagulants is likely to be low. One of the falcons released by the FFG project died of kidney failure months after being exposed to the chemicals placed in a footbath for treating foot-rot in sheep (M. Jesson, personal communication). This individual had been imprinted on humans at the time of release, so better pre-release conditioning may have prevented her from being exposed to the poison. However, the presence of poisons in unsupervised treatment containers around the country could pose a threat to many individual birds.

3. I found that introduced predators attacked artificial and real falcon nests in a vineyard landscape less often than in a wild habitat, and that the predators (hedgehogs and harriers) that did target falcon nests in vineyards posed less of a threat to falcons than the larger and more voracious predators (stoats and cats) in the hill habitat (Chapter 7). These results lend support to the theory that an agricultural landscape could lend itself to the conservation of threatened species. However, further research into predator abundance in these two habitats using trapping is needed to corroborate these results.

CONCLUSION

I found that falcons reintroduced into vineyards provided economically valuable biological control services, while the vineyards themselves offered falcons high prey abundance and fewer dangerous introduced predators compared to the hill habitat from which they were translocated. Falcons nesting in vineyards showed higher nest attendance rates and fed their chicks more, while released juveniles were able to develop flight and hunting skills at a similar rate to their wild-raised counterparts. The findings from my research therefore support the theory that conservation initiatives need not be restricted to dwindling natural reserves, and can be extended into agricultural landscapes.

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APPENDIX ONE

SUMMARY OF VARIABLES RETAINED IN THE MODEL FOR OVERALL GRAPE DAMAGE

(See Chapter 2 for details)

Appendix 1

	Overall Damage			
	Estimate	SE	t value	P
(Intercept)	-2.851	0.48	-5.933	<0.001
Falcon Present	-1.201	0.26	-4.595	<0.001
Interior Vines	-1.446	0.31	-4.720	<0.001
Pinot Noir	0.283	0.35	0.799	0.425
Half canopy	-0.188	0.08	-2.288	0.022
Full Canopy	-1.064	0.12	-8.899	<0.001
Bird Scaring 1-5	No significant values (all $p > 0.2$)			
Direction (north)	0.234	0.26	0.907	0.365
Direction (south)	-0.086	0.26	0.907	0.744
Direction (west)	-0.003	0.05	-0.072	0.943
Distance from bird shelter (m)	Removed from simplified model			
PCA1	-0.378	0.06	-5.834	<0.001
PCA2	0.071	0.06	1.171	0.242
PCA3	0.272	0.07	3.774	<0.001
Falcon Present: Interior Vines	-0.142	0.61	-0.234	0.815
Falcon Present: Pinot Noir	0.829	0.46	1.789	0.074
Interior Vines: Pinot Noir	1.639	0.52	3.142	0.002
Falcon Present: half canopy	0.201	0.15	1.336	0.182
Falcon Present: full canopy	0.028	0.22	0.131	0.896
Interior vines: half canopy	0.328	0.25	1.335	0.182
Interior vines: full canopy	-0.429	0.43	-0.986	0.324
Pinot Noir: half canopy	-0.176	0.18	-0.978	0.328
Pinot Noir: full canopy	0.528	0.36	1.466	0.143
Falcon Present: interior vine: Pinot Noir	-1.028	0.89	-1.159	0.247
Falcon Present: interior vine: half canopy	-0.298	0.66	-0.455	0.649
Falcon Present: interior vine: full canopy	-0.668	1.31	-0.511	0.610
Falcon present: Pinot Noir: half canopy	-0.026	0.27	-0.097	0.923
Falcon present: Pinot Noir: full canopy	-0.452	0.52	-0.876	0.381
Interior vine: Pinot Noir: half canopy	0.538	0.38	1.412	0.158
Interior vine: Pinot Noir: full canopy	-20.649	32810	-0.001	0.995
Falcon present: interior: Pinot Noir: half canopy	-1.067	0.88	-1.213	0.225
Falcon present: interior: Pinot Noir: full canopy	21.845	32810	0.001	0.995

The intercept represents sites with no falcon present, edge vines, Sauvignon Blanc variety, no canopy cover, east-facing vines, no bird scaring, no PCA input and 0m from nearest bird shelter. Colons (:) between two terms represent an interaction effect within the model, Appendix 2 shows the makeup of each PCA axis. Overall damage was modelled using a generalised linear mixed model with binomial errors and a logit link function and simplified using AIC. We tested for overdispersion based on the ratio of residual deviance to degrees of freedom, and upon finding evidence of overdispersion, we re-analysed the best-fit model using penalised quasi-likelihood generalised linear mixed models with quasi-binomial errors. To convert the estimates to true proportions the values need to be inverse-linked ($e^{\eta} / (1 + e^{\eta})$) as we have done in Table 2.1.

APPENDIX TWO

SHORT NOTE: ACCOUNTS OF BIRD ELECTROCUTIONS IN NEW ZEALAND

Mortality from electrocution on power structures is a major threat to birds in human-modified landscapes around the world. Because of their large size and preference for perching from high vantage points, raptors are especially prone to electrocution (Lehman et al. 2007). Globally, agricultural expansion and intensification has drastically changed landscapes (Foley et al. 2005). While some species of raptor can take advantage of the large food sources available in agricultural landscapes, the low availability of natural perches and high frequency of electricity structures in these regions can lead to a high incidence of electrocution, sufficient to limit population growth (Real et al. 2001; Marchesi et al. 2002; Sergio et al. 2004; Lehman et al. 2007). Following reports of New Zealand falcon being electrocuted throughout Marlborough (Fox & Wynn 2010), I contacted a number of organisations and individuals to identify which species are electrocuted and to determine how widespread the problem is.

This is the first attempt to collect information on the electrocution of native birds across the country. Reports of birds either found dead under electricity structures or found with burns to their feet or bodies (Table A.1) were available for twenty-three birds of nine species throughout New Zealand. This suggest that, in a country with a high proportion of threatened native species, power lines and transformers are dangerous to a wide range of New Zealand's larger birds. As a consequence of this collation of information, Department of Conservation (DoC) offices and rehabilitation centres are now watching out for signs of electrocution, including blackened feet.

The majority of birds that are electrocuted are unlikely to be found, so the number and widespread geographical range of the reports in Table 1 is indicative of a larger problem. Evidently, more effort is needed to quantify the danger of electro-utility structures to New Zealand's avifauna. In order to obtain an accurate idea of electrocution-induced avian mortality it is important that people picking up dead birds take note of any visible injuries and also of any nearby power lines and that a repository exists for this information. Details of the location of the dead bird are important because, aside from being found under power lines or poles, some electrocuted individuals show no physical signs of electrocution. For example a 3-year-old Kaka found in Northland (Table A.1) was found dead under a power pole mounted with a

transformer, and was autopsied and found to be in good condition with a full-crop and no signs of trauma (S. Phillips, personal communication). In other cases, signs of electrocution can be obvious. For example, a kereru in Southland was found with both legs burnt off and burn marks over much of its body (R. Powlesland, pers. comm.). Additionally, birds that are electrocuted are not always killed immediately (Fox & Wynn 2010), as was the case for a fledgling kea at Aoraki/ Mt. Cook village. This bird was electrocuted at an electrical substation, causing a power blackout. It was located alive 3 days later, but was later euthanized to relieve suffering from necrotic flesh wounds (R. Schwing, pers. comm.).

Retrofitting dangerous structures can be a successful means of mitigating fatalities due to electrocution (López-López et al. 2011). Transformers appear to be the most dangerous structures for perching birds (Table A.1). Electro-utility structures with multiple live components close together, or those that have grounded hardware are more likely to electrocute birds (Lehman et al. 2004). Transformer boxes in many parts of New Zealand are connected to the overhead transmission lines via un-insulated wires that are connected to the grounded transformer. Birds can form a circuit by perching on the transformer box and touching any one of the wires, or by touching two wires as they come close to each other in order to enter the transformer box. In Marlborough, retrofitting transformers by placing thick rubber casings around the wires has been trialled, but is an expensive process, costing between $200 and $400 per transformer. Much of this cost is likely to be in labour, and it would therefore be wise to retrofit transformers whenever they are worked on for other reasons. This long-term solution would result in considerably less cost to power companies and consumers. In the meantime, in open areas such as agricultural regions, transformers identified as dangerous could be retrofitted on a case-by-case basis by identifying factors that make certain poles more hazardous to perching birds (see Mañosa 2001). Physical deterrents such as spikes or bars may also hold promise, and could potentially be a cheaper alternative, but would require extensive testing prior to widespread use, as some deterrents are not successful (Prather & Messmer 2010).

Table A.1. Reports of birds collected dead under power lines or found after being electrocuted.

Species	Year	# individuals	Location	Found beneath	Reported by
New Zealand falcon (*Falco novaeseelandiae*)	2009	1	Glenorchy, Otago	Transformer	Barry Lawrence
	2010	1	Ngakuta Bay, Marlborough	Transformer	Dianne John
	2010	2	Glenorchy, Otago	Transformer	Barry Lawrence
	2010	1	Wairau Valley, Marlborough	Transformer	Colin Wynn
Australasian harrier (*Circus approximans*)	2010	1	Wairau Valley, Marlborough	Transformer	Mike Bell & Phil Bradfield
	2010	1	Wairau Valley, Marlborough	Transformer	Sara Kross
Kea (*Nestor notablis*)	2009	1	Mt Cook Village, South Canterbury	Substation	Raoul Schwing
Kaka (*Nestor maridionalis*)	2009	1	Whakatane	Power lines	John Groom
	2010	1	Parua Bay, Whangerei, Northland	Transformer	Suzi Phillips
Kereru (*Hemiphaga novaeseelandiae*)	1998	1	Southland	Unknown-definite electrocution	Ralph Powlesland
	2005	2	Southland	Power pole (possible electrocution)	Ralph Powlesland
	2006	3	Southland	Transformer	Lloyd Esler
Eastern rosella (*Platycercus eximius*)	2010	1	Whakatane	Transformer	Rosemary Tully
Canada goose (*Branta Canadensis*)	1992	4	Auckland	Power line & transformer	Graham Jones
Magpie (*Gymnorhina tibicen*)	~1990	1	Invercargill	Transformer	Sally Dunston
Black swan (*Cygnus atratus*)	2009	1	Awatere valley, Marlborough	Power line	Sara Kross
Cooks petrel (*Pterodroma cookii*)	2009	1	Whakatane	Power line	Rosemary Tully

Cause of death is deduced from the location under which birds were found. Transformer electrocutions are for birds that were found dead under power poles mounted with transformers, but it is possible that another connection on the same pole caused the electrocution. Birds found under power poles may actually have been found under a transformer pole but were not noted by the collector. Similarly, birds found under power lines are likely to have died from collision, but electrocution may be a possibility, as nearby transformers may not have been noted by the collector. The kea was seen to be electrocuted while within an electrical substation.

Acknowledgements

P. Gaze assisted with accessing reports of electrocutions and provided advice. The individuals listed in Table 1 scoured through old records to report on past bird electrocutions and are thanked for their contributions. X. Nelson provided helpful comments on the manuscript.

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APPENDIX THREE

PUBLISHED VERSION OF CHAPTER 2

Kross, S.M., Tylianakis, J.M., & Nelson, X.J. 2012. Effects of Introducing Threatened Falcons into Vineyards on Abundance of Passeriformes and Bird Damage to Grapes. *Conservation Biology*. 26: 142-149. doi: 10.1111/j.1523-1739.2011.01756.x

APPENDIX FOUR

PUBLISHED VERSION OF CHAPTER 3

Kross, S.M. & Nelson, X.J. 2011. A portable low-cost remote videography system for monitoring wildlife. *Methods in Ecology and Evolution,* **2,** 191-196.

APPENDIX FIVE

PUBLISHED VERSION OF CHAPTER 5

Kross, S.M., Tylianakis, J.M. & Nelson X.J. 2012. Translocation of threatened New Zealand falcons to vineyards increases nest attendance, brooding and feeding rates. PLoS ONE 7(6): e38679. doi:10.1371/journal.pone.0038679

OPEN ACCESS Freely available online

PLoS one

Translocation of Threatened New Zealand Falcons to Vineyards Increases Nest Attendance, Brooding and Feeding Rates

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Abstract

Anthropogenic landscapes can be rich in resources, and may in some cases provide potential habitat for species whose natural habitat has declined. We used remote videography to assess whether reintroducing individuals of the threatened New Zealand falcon *Falco novaeseelandiae* into a highly modified agricultural habitat affected the feeding rates of breeding falcons or related breeding behavior such as nest attendance and brooding rates. Over 2,800 recording hours of footage were used to compare the behavior of falcons living in six natural nests (in unmanaged, hilly terrain between 4 km and 20 km from the nearest vineyard), with that of four breeding falcon pairs that had been transported into vineyards and nested within 500 m of the nearest vineyard. Falcons in vineyard nests had higher feeding rates, higher nest attendance, and higher brooding rates. As chick age increased, parents in vineyard nests fed chicks a greater amount of total prey and larger prey items on average than did parents in hill nests. Parents with larger broods brought in larger prey items and a greater total sum of prey biomass. Nevertheless, chicks in nests containing siblings received less daily biomass per individual than single chicks. Some of these results can be attributed to the supplementary feeding of falcons in vineyards. However, even after removing supplementary food from our analysis, falcons in vineyards still fed larger prey items to chicks than did parents in hill nests, suggesting that the anthropogenic habitat may be a viable source of quality food. Although agricultural regions globally are rarely associated with raptor conservation, these results suggest that translocating New Zealand falcons into vineyards has potential for the conservation of this species.

Citation: Kross SM, Tylianakis JM, Nelson XJ (2012) Translocation of Threatened New Zealand Falcons to Vineyards Increases Nest Attendance, Brooding and Feeding Rates. PLoS ONE 7(6): e38679. doi:10.1371/journal.pone.0038679

Editor: Adam Stow, Macquarie University, Australia

Received January 6, 2012; **Accepted** May 14, 2012; **Published** June 14, 2012

Funding: This research was supported by a University of Canterbury Doctoral Scholarship (to S.M.K.) and grants from the Brian-Mason Scientific & Technical Trust (to S.M.K. and X.J.N.; www.brianmasontrust.org) and Canon New Zealand (to S.M.K.). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared this research was supported by Canon New Zealand (to S.M.K.). This does not alter the authors' adherence to all the PLoS ONE policies on sharing data and materials.

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Introduction

Agricultural expansion and intensification is a principal contributor to habitat change [1] and represents the "greatest extinction threat to birds" [2]. Raptor species worldwide have suffered declines [3], largely as a result of anthropogenic activities linked with agriculture, such as land clearing and the use of poisons for pest control [4]. Additional causes of mortality include persecution as a result of human-wildlife conflict and electrocution on electro-utility structures [5–7].

Raptor declines can be mitigated through the reintroduction of individual birds from their strongholds in order to bring threatened species back to their historic ranges [8]. Reintroductions have been successfully used to expand the ranges of a number of threatened raptors worldwide [9–10]. However, release sites for reintroduction programs normally comprise regions of natural habitat from which raptors have become extirpated. With land increasingly being put to use for anthropogenic purposes, there is inevitably a conflict when land is set aside for conservation. Consequently, there have been calls for increasing biodiversity conservation outside of the traditional reserve system [11]. Conservation efforts could be considered within primary production systems [12–13] by using farming practices that are more wildlife-friendly [2], provided that the species in question can survive within such agricultural landscapes.

There is extensive variability in how well raptors adjust to human landscapes, with some species being unable to inhabit modified habitats while others show considerable flexibility in this regard [14]. Conservation scientists have traditionally been slow to incorporate animal behavior when developing sustainable conservation management plans and policy [15–16], and this lack of consideration of the behavior of the animal in question has sometimes resulted in failed reintroductions [17]. As the ability of translocated individuals to display adaptive behavior in novel environments can influence the success of reintroduction projects, it should be examined closely at the onset of a reintroduction [8,15–18]. This need to assess the behavioral ramifications of translocation is particularly acute when animals are reintroduced into anthropogenic landscapes. In these landscapes, translocated individuals must be able to forage, find shelter, and reproduce in order for a reintroduction program to succeed [9,17–18].

In Marlborough, New Zealand's largest wine-growing region, there is an intensive monoculture of vineyards spread throughout the valleys that were once inhabited by the now threatened New

Zealand falcon, *Falco novaeseelandiae*, the country's only remaining endemic bird of prey [19]. To combat the decline of falcons in Marlborough a project called 'Falcons For Grapes' (FFG) was established in 2005 to reintroduce falcons into the vineyard-dominated valleys of the region [20,21]. As its name suggests, this project aims to use falcons to benefit the wine industry through their release into vineyards, while at the same time benefitting falcons through access to higher prey densities in vineyards and an expansion of their range [21]. Recent work has shown that falcon presence in vineyards is associated with considerable economic savings through a reduction in grape damage caused by passerine birds [22]. However, whether there is a simultaneous benefit to the falcon population is, as yet, unknown. Although vineyards have high densities of potential vertebrate prey (particularly European birds), falcons relocated to vineyards are also enticed to stay through supplementary feeding schemes.

The FFG project presented us with a unique opportunity to do a comparative analysis of the breeding behavior of reintroduced falcons in vineyards with falcons found in the nearby hills. We use these comparative data to compare the chick-rearing behavior and ability of falcons reintroduced into vineyards with that of falcons breeding naturally within the surrounding hill habitats. Falcon chicks hatch at roughly 31 g and reach full adult weight (330 g for males, and 531 g for females) in a 35-day rearing period [23]. This necessitates that adult falcons provision chicks with a large amount of prey each day. Feeding rates during the chick-rearing period dictate chick survival and contribute heavily to breeding success rates and population trends [24]. We therefore focused our study on comparing the food provisioning rates and the biomass of prey items delivered to falcons in both the vineyards and hills.

Generally, raptor species share biparental care duties during incubation and when their altricial chicks first hatch [24]. Extrinsic factors, such as habitat quality and prey abundance, may influence the time budget allocated by raptors to different activities and thus potentially affect breeding success [25]. Parents must balance the need to feed their young against the increased exposure of young to potential nest predation while their parents are foraging. New Zealand falcons nest in scrapes on the ground, and their nests are vulnerable to high levels of predation, mainly by introduced mammals such as feral cats (*Felis felis*) and stoats (*Mustela erminea*) [Kross SM, Tylianakis JM, Nelson XJ unpublished manuscript]. Areas of high prey density may therefore benefit falcons considerably through a reduction of time spent searching for prey, with a concomitant increase in nest attendance rates which may be associated with higher nesting success, as found in peregrine falcons (*Falco peregrinus*) [25].

Here, we provide evidence of the impact of anthropogenic habitat on prey provisioning rates, parental nest attendance, and brooding rates at nests of the threatened New Zealand falcons. By examining how the parental behavior of the New Zealand falcon differs between hill and anthropogenic vineyard habitats, we provide further evidence that behavioral studies should be inextricably tied to the implementation of sustainable conservation management plans.

Methods

Ethics Statement

This research was conducted according to relevant national and international ethics guidelines and permits were provided by the University of Canterbury (2008/27R) and the New Zealand Department of Conservation (NM-23677-FAU).

Study Species

Despite its threatened status, little is known about the breeding behavior of the New Zealand falcon. New Zealand falcons evolved in the absence of land-dwelling mammals, and therefore lack the morphological and behavioral adaptations necessary to deal with mammalian predators [26]. For example, they often nest in 'scrapes' on the ground, making them prone to high levels of nest predation [23,27–28]. In the New Zealand falcon, incubation lasts for 30 days, followed by a 30–35 day rearing period during which chicks develop the ability to thermoregulate (at approximately 12 days), reach full adult weight (at approximately 20 days), and develop feathers. Adult females undertake the majority of nest attendance, nest defense, and feeding of chicks, while male falcons assume most of the foraging and provision females and chicks with food [23]. As chicks grow, female falcons begin to take part in foraging and food provisioning [23].

Falcon nests were located by interviewing local farmers and forestry workers. Non-vineyard falcon nests ('hill nests') were found either in hillside forestry plantations (*Pinus radiata*) or in steep-sided valleys dominated by a mix of native and introduced grasses and dense scrub [28]. In contrast, vineyard falcon nests ('vineyard nests') were near the valley floor, usually within a vineyard, although on one occasion, within a forestry plantation adjacent to a vineyard. The key differences between the nest types were that vineyard adults were manipulated by the FFG project, whereas hill adults were not manipulated. Vineyard adults had been translocated into the vineyards as juveniles, were offered supplementary food on a daily basis (one-day-old poultry chicks), and had their nests raised from the ground into artificial nests in order to reduce the chances of predation by invasive mammals. Over 50 falcons were released by the FFG project in the valleys of Marlborough between 2005 and 2011, and eight have been confirmed to breed within the vineyard region, including the four vineyard nests that we monitored for this study (R. Seaton, pers. comm.).

Data Collection

Our data were based on footage obtained from six hill nests (101 days or 1473 recording hours) and four vineyard nests (88 days or 1333 recording hours) monitored between 2008 and 2011. We were only able to monitor five of the eight confirmed breeding falcons that were released as part of the FFG project because the remaining nesting events were before our study period, were outside of the vineyard region, or failed before we could monitor them. We used a portable remote videography system with a near-infrared camera placed at the edge of the nest or mounted to the side of nest barrels in the case of vineyard nests. The system was set to record (at 30 fps) based on a motion-detection threshold of 10–15%, and has been shown to lose only 16% of potential recording hours, primarily due to battery failure or camera dislodgement [28]. For these data, if over 50% of recording hours in any given day were missed, that day was excluded from the dataset. Video was reviewed using Quick-Time Player (version 7.6.4; Apple Inc, Cupertino, CA, USA) at a maximum speed of four times normal speed to a minimum speed of frame-by-frame, allowing quick review of non-important files and detailed review of important events, such as feeding.

Monitored nests during the chick rearing stage had 1, 2, or 3 chicks. The number of chicks in these nests did not differ significantly between hill ($n = 13$) and vineyard ($n = 8$) nests (Mann Whitney $U = 12.0$, $P = 0.91$; for both habitats median $= 2.0$; 1st and 3rd quartiles are 1.0 and 3.0). In the rare (i.e. $<10\%$ of recordings) cases where one or more of the chicks had moved outside of the recording area, we stipulated that at least one chick had to be fully visible to the camera to be included in the dataset.

We recorded the duration of parental behaviors (see Table 1) by scoring the start and end time of each behavior, and used these numbers to calculate duration. In all cases we recorded the sex of the individual engaged in the behavior. Additionally, we recorded the number of nest disturbances by people or other animals per day, and used an ordinal scale of 0–10 (with 10 being the highest and equivalent to something entering the falcon's nest) to measure the level of each disturbance to the nesting falcons (Table S1). The disturbances were considered to be additive per day; for example, if a nest was entered two times in one day, the disturbance level for the day would be equal to 20.

Over half of the prey items delivered to the nest could not be identified to species and we estimated the biomass of these items by comparing the size of the prey item with previous, positively identified prey items. The one-day-old poultry chicks (c. 40 g) provided as supplementary food were larger than the finch and bunting species commonly consumed by falcons [Kross SM, Tylianakis JM, Nelson XJ unpublished manuscript] and, because they were easily identifiable due to their bright yellow color, all were identified when they were delivered to chicks. We collected information on the amount of prey handling that occurred prior to items being delivered to the nest by the parents. Avian prey were aged according to feather structure: birds with completely sheathed feathers were considered nestlings, those with partially sheathed feathers were considered fledglings, and those with unsheathed feathers were considered adults [29]. The amount of prey handling done prior to parents delivering the item to chicks was noted, with prey being either completely plucked (no wing or tail feathers remaining), partially plucked (some wing or tail feathers remaining) or not plucked (all wing and tail feathers intact). We also noted the presence or absence of the preys' head at the time of delivery to the nest.

Data Analysis

Data from individual nests were analyzed with increasing chick age in days as a predictor variable, defined using the hatching date as chick age 0. In order to maximize data collection for all chicks, data were collected until day 30; the age at which chicks begin to fledge from the nest [23]. Daily data recording began at 05:00 and ended at 21:00. These times were chosen because feeding events never occurred prior to 5 am, and out of a total of 2026 feeding events recorded, only 11 occurred after 9 pm (i.e., 99.5% of feeding events occurred during these hours).

We examined parental time budgets by calculating the proportion of the recorded daylight hours adult falcons spent feeding chicks, in attendance at the nest, brooding chicks, or performing nest maintenance. These data were then transformed using a logit transformation [30], and modeled using generalized linear mixed effects models (GLMMs) with Gaussian errors in the lme4 package [31] in R (v.2.7.2) [32]. We were unable to use binomial errors because our proportion time data were not derived from proportions of successes/failures in a fixed number of independent binary trials. Separate models were analyzed for male and female adult falcons, and for both parents combined. The average time between feeding events, the average biomass of prey items, and the average total biomass fed to chicks per day were all modeled using GLMMs with Gaussian errors.

Counts for the amount of nest activity (occasions where parents left the nest), the number of feeding events, and the level of disturbances per day were all modeled using GLMMs with Poisson errors. Feeding data were first analyzed including items identified as supplementary food, and then were analyzed excluding items identified as supplementary food.

Site (i.e. nest identity), the identity of the female and the identity of the male parent were fitted as random effects in all GLMMs. The identity of the parents was included as a random effect to control for non-independence of data between nests containing the same individual male or female falcon (across years, no two nests contained the same pair of adult falcons, but in a few cases either a male or female was paired with a different mate at a different nest site location). We included habitat type, the number of chicks in the nest, and level of disturbances as categorical fixed effects in the models. Chick age in days was included as a continuous fixed effect in the models. We also included an interaction term between chick age and habitat type, as well as quadratic and cubic polynomial terms for chick age in the models to account for potential nonlinear effects of chick age (e.g., asymptotes or step-changes in behavior once a threshold age is reached).

Models were simplified by sequentially removing non-significant polynomial and interaction terms then main effects until no improvement in model fit (measured using the Akaike Information Criterion, AIC) was obtained. We tested all Poisson models for evidence of overdispersion (on the basis of the ratio of residual deviance to degrees of freedom) and re-fitted overdispersed models using penalized quasi likelihood (the 'glmmPQL' function) in the MASS package [33] in R. For models fitted using Gaussian errors

Table 1. Parental behavior recorded at each falcon nest.

Behavior	Description	Data obtained for analysis
Nest attendance	Time spent by adults in the nest, including being engaged in all of the behaviors below, as well as when in the nest, but not touching chicks or engaging in other defined behavior.	Proportion of the daily total(s).
Nest activity	Number of times adult falcons departed the nest; used as a proxy for activity at the nest entrance (see [25]).	Counts.
Brooding	Adult falcon is physically touching at least one chick with breast, tail, or wings. Also applies if falcon is standing over chicks to provide shade (stress brooding).	Proportion of the daily total(s). Count of brooding bouts. Average length of brooding bouts.
Nest maintenance	Adult falcon is pulling at substrate within scrape. Also applies to removing items such as prey remains.	Proportion of the daily total(s).
Feeding	Adult falcon is feeding food to chicks or is eating.	Proportion of the daily total(s). Counts of feeding events. Average time(s) between feeding events. Average biomass (g) of individual prey items. Sum of prey biomass (g)

doi:10.1371/journal.pone.0038679.t001

we used a Markov chain Monte Carlo (MCMC) resampling method with 10,000 simulations to estimate P values for the fixed effects (carried out using the 'pvals.fnc' function in the languageR package [34] in R). We used Student's t-tests to compare the prey handling behavior and the age classes of prey for falcons in the two habitats, as well as to compare the number and level of disturbances by people or animals at the nests. In our results, where relevant, we present the mean (± SD) for untransformed data (as a measure of effect size) in addition to P and ± SE values from model estimates.

Results

Feeding Behavior

The number and level of nest disturbances by people or animals did not differ significantly between the two habitats ($t = -0.51$, $P = 0.63$). In vineyard nests, supplementary food items represented 17.89%±8.94% of prey items adults provisioned to their chicks. At three of the vineyard nests, supplementary food items represented <10% of the prey items brought to chicks. However, at the fourth nest, supplementary food items represented 44.53% of prey items brought to chicks.

Falcons from nests in the hills spent a significantly lower proportion of their time feeding chicks than did falcons nesting in vineyards (Table 2; Figure 1). Feeding decreased as chicks aged, although more so in hill nests than in vineyard nests (habitat x chick age interaction: Table 2; Figure 1). In hill nests, parents increased the proportion of the day spent feeding from chick hatching until chicks were approximately 9 days old, after which they began to decrease. In vineyard nests, this switch occurred later, when chicks were approximately 12 days old (quadratic polynomial term; Table 2; Figure 1).

Vineyard and hill nests did not differ significantly in the interval between feeding bouts (Table 2). Regardless of habitat type or chick age, nests containing a greater number of chicks experienced less time between feeding bouts (Table 2). The number of feeding events per day was also influenced by habitat type and chick age. In both habitats, as chick age increased, male falcons delivered more food items to the chicks, starting at an average of 0.03 feedings per day when chicks first hatched and increasing by 0.04 feedings for each day as chicks aged (Table 2). Female falcons in vineyard nests also increased their number of feeding events as chick age increased, starting at an average of 8.89 feedings per day when chicks first hatched and increasing by 0.10 feedings per day as chick age increased (Table 2). In contrast, females in hill nests started at an average of 9.44 feeding events per day when chicks first hatched, but decreased the number of feedings by 0.20 per day as chick age increased (Table 2). When supplementary food was excluded from the analysis, nests in the hills had an average of 1.41 more feeding events per day (Table 2) compared with vineyard nests. Removing supplementary food from the analysis did not change the fact that, compared with nests with one chick, nests containing 2 chicks and 3 chicks received more food (2.44 and 4.73 more feeding events per day, respectively; Table 2). The quadratic polynomial for chick age was retained in the final model for the number of feeding events, suggesting a nonlinear relationship, but was removed from the final model excluding supplementary food, suggesting a linear relationship.

At the time of hatching, there was no effect of habitat type (Table 2) on the average biomass of each individual prey item consumed by chicks (hill, 23.56±3.31 g; vineyard, 20.00±2.51 g). However, as chick age increased, the average biomass of prey items in vineyard nests increased, while the average biomass of prey items in hill nests decreased slightly (chick age x habitat interaction, Table 2). Excluding supplementary food (mean biomass of a day-old poultry chick was 40 g) from this analysis reduced the average biomass slightly in vineyard nests (17.98±2.55 g) at the time of hatching, but there remained no significant effect of habitat type in our model (Table 2). Even with supplementary food excluded from the analysis, the average biomass of prey items increased in vineyard nests, but decreased in hill nests (chick age x habitat interaction, Table 2).

The total biomass of prey fed to chicks each day was the sum of all prey items. When chicks first hatched there was no statistically significant difference in the total biomass fed to them in the different habitat types, but as chicks became older, there was an increasing difference between hill and vineyard nests, with vineyard nest parents feeding chicks an additional 7.58 g per day (chick age effect: Table 2), while parents from the hill nests only fed an additional 2.42 g per day (habitat x chick age interaction: Table 2; Figure 2). Nests with more chicks were also given more food. Keeping all other variables constant, nests with 1 chick received a daily mean ± SEM of 101.59±37.54 g, those with 2 chicks 256.04±63.25 g, while those with 3 chicks received 250.55±27.84 g of food (Table 2). Excluding supplementary food items from the analysis for total biomass reduced the overall estimates for biomass fed to chicks, but did not change the lack of statistically significant differences between habitat types (Table 2). Excluding supplementary food resulted in a non-significant relationship between habitat type and chick age (Table 2). Disregarding supplementary food did not change the positive effect of chick age, or number of chicks in the nest on total biomass, but did slightly reduce the scale of these estimates (Table 2).

Prey handling (i.e. whether the parents had plucked the feathers or fur from their prey or decapitated their prey) was influenced by habitat. A greater proportion of the bird prey delivered to vineyard nests was completely plucked (70.38±2.97%) compared with hill nests (56.10±3.92%, $t = 2.90$, $P = 0.02$). Hill falcons brought their chicks a greater proportion of partially plucked (21.48±2.88%) and unplucked (17.08±4.54%) avian prey compared with vineyard falcons (15.67±2.96% and 12.32±2.41% respectively) although these differences were not statistically significant (partially plucked: $t = 1.41$, $P = 0.2$; not plucked: $t = 0.92$, $P = 0.4$). Falcons in vineyard nests decapitated more of the prey items delivered to chicks (68.59±3.29%) than falcons in hill nests (56.31±2.22%, $t = 3.10$, $P = 0.02$).

Only 42.45% of prey items delivered to nests were identified to age class. The diet of falcons in vineyards consisted of a higher proportion of juvenile avian prey (vineyard mean = 5.19±1.94%, hill mean = 1.28±0.73%, $t = 3.86$, $P = 0.02$), but the two habitats were similar in the proportion of adult (mean = 27.98±11.27%, $P > 0.30$) and nestling (mean = 10.91±5.23%, $P > 0.80$) prey items in the diets fed to chicks.

Chick-rearing Behavior

Nest attendance, the proportion of the day that at least one adult was present within the nest scrape (Table 3), was 3.3% lower for parents in hill nests than in vineyard nests (Table 3, Figure 3) and significantly decreased as chicks aged in both habitat types (Table 3, Figure 3). This relationship with age was nonlinear, with the rate of this decline tending to slow after chicks reached approximately 20 days old, and both polynomial terms for chick age were retained in the simplified model (Table 3, Figure 3). This effect was largely due to the behavior of female parents, which were responsible for the majority of nest attendance over the chick-rearing period (Table 3, Figure 3).

Table 2. Generalized linear mixed effects model coefficients for feeding parameters measured for breeding New Zealand falcons *Falco novaeseelandiae* nesting in managed vineyards and unmanaged hill habitat.

Response variable		Intercept	Effect of habitat (hill nests)	Effect of chick age (per day)	Effect of interaction between habitat and chick age	2 chicks in brood	3 chicks in brood	Quadratic polynomial term	Cubic polynomial term
Proportion of day spent feeding chicks	Estimate	0.15	0.08 (−0.06)	0.15 (−0.005)	R	R	R	0.15 (<0.001)	R
	t-value	−6.64	−2.12	−6.82				−7.97	
	p-value	<0.001	0.04	<0.001				<0.001	
Interval between feeding bouts (sec)	Estimate	6339.36	7180.40 (841.04)	6313.80 (−25.56)	6309.36 (−29.532)	4363.34 (−1976.03)	3273.99 (−3065.37)	6348.48 (9.119)	6339.05 (−0.311)
	t-value	9.554	1.313	−0.807	−1.132	−2.346	−6.992	5.815	−1.457
	p-value	0.0010	0.2314	0.4376	0.2612	0.0418	0.0001	0.0001	0.1660
Number of feeding events per day by female	Estimate	8.89	9.44 (0.55)	8.99 (0.10)	8.79 (−0.10)	13.23 (4.39)	12.81 (3.92)	8.87 (−0.02)	R
	t-value	19.01	0.43	2.64	−3.33	2.77	5.00	−5.93	
	p-value	<0.001	0.67	0.008	<0.001	0.006	<0.001	<0.001	
Number of feeding events per day by male	Estimate	0.036	R	0.041 (0.005)	R	0.08 (0.04)	0.15 (0.11)	0.035 (−0.001)	R
	t-value	−7.88		7.58		1.21	4.27	−2.20	
	p-value	<0.001		<0.001		0.23	<0.001	0.03	
Number of feeding events by both parents	Estimate	7.00	7.12 (0.12)	R	R	9.76 (2.76)	11.04 (4.04)	6.99 (−0.01)	R
	t-value	23.76	5.26			2.77	6.62	−4.47	
	p-value	<0.001	<0.001			0.006	<0.001	<0.001	
Number of feeding events without supplementary food	*Estimate*	*5.94*	*7.35 (1.41)*	*6.01 (0.07)*	*R*	*7.51 (1.57)*	*7.92 (1.98)*	*R*	*R*
	t-value	*20.85*	*3.48*	*3.84*		*2.44*	*4.73*		
	p-value	*<0.001*	*<0.001*	*<0.001*		*0.01*	*<0.001*		
Mean biomass of prey items	Estimate	20.00	23.56 (3.56)	20.28 (0.28)	19.89 (−0.10)	R	R	R	R
	t-value	7.97	1.08	2.96	−2.70				
	p-value	<0.001	0.29	0.007	0.011				
Mean biomass of prey items (supplementary food removed)	*Estimate*	*17.98*	*23.58 (5.60)*	*18.28 (0.30)*	*17.88 (−0.10)*	*R*	*R*	*R*	*R*
	t-value	*7.04*	*1.66*	*3.11*	*−2.78*				
	p-value	*<0.001*	*0.11*	*0.003*	*0.006*				
Total daily biomass	Estimate	101.59	118.51 (16.91)	109.18 (7.58)	104.01 (2.42)	256.04 (154.95)	250.55 (148.95)	101.06 (−0.53)	R
	t-value	2.71	0.38	8.41	−3.82	2.44	5.35	−6.62	

Table 2. Cont.

Response variable		Intercept	Effect of habitat (hill nests)	Effect of chick age (per day)	Effect of interaction between habitat and chick age	2 chicks in brood	3 chicks in brood	Quadratic polynomial term	Cubic polynomial term
	p-value	0.011	0.72	<0.001	<0.001	0.18	<0.001	<0.001	
Total daily biomass without supplementary food	*Estimate*	*87.69*	*155.66 (67.97)*	*92.51 (4.82)*	*89.88 (2.19)*	*197.14 (109.45)*	*168.22 (80.54)*	*87.30 (−0.38)*	*R*
	t-value	*2.95*	*1.92*	*4.98*	*− 1.82*	*2.53*	*3.93*	*−4.41*	
	p-value	*0.016*	*0.083*	*<0.001*	*0.076*	*0.031*	*<0.001*	*<0.001*	

Models for count data were analyzed using Poisson errors, and all other data were logit transformed and modelled using Gaussian errors. Supplementary food items were provided to falcons nesting in vineyards on a daily basis and weighed an average of 40 g. Models for data where supplementary food items have been removed are shown in italics. Values shown in parentheses under estimates show the change from the model intercept. R = Predictor variable removed during model simplification.

doi:10.1371/journal.pone.0038679.t002

There was no effect of habitat on the time parents spent brooding chicks. Immediately after hatching, parents in both habitats spent 93.70% of the day brooding (Table 3). In both habitat types, adults significantly decreased the proportion of time spent brooding as chicks aged (Table 3), although this effect was nonlinear, with the slope of the decline leveling out at close to zero once chicks reached approximately 18 days old (quadratic and cubic polynomials Table 3).

The amount of nest activity (the number of times parents left the nest) at vineyard nests was significantly higher than at hill nests, with parents at vineyard nests leaving the nest more frequently (21.84 ± 8.12 daily nest exits) than in hill nests (17.10 ± 6.01 daily exits; Table 3). When chicks first hatched, parents in vineyard nests averaged 33.6 nest exits/day, while those in hill nests averaged 26.1 nest exits/day. However, as chick age increased, parents in both habitats significantly decreased activity around the nest (Table 3), particularly after chicks reached approximately 11 days old (second order polynomial for chick age, Table 3).

There was no effect of habitat on the small proportion of the time per day spent maintaining nests (hill, 0.01 ± 0.02; vineyard, 0.01 ± 0.01) and the habitat term was removed from the simplified model. In both habitat types, adults significantly decreased the time spent maintaining nests as chicks aged (Table 3).

Discussion

Reintroducing the New Zealand falcon into the vineyards of Marlborough has previously been shown to successfully provide vineyards with a natural form of pest control, by reducing the abundance of pest birds (starlings *Sturnus vulgaris;* song thrushes *Turdus philomelos*; and blackbirds *Turdus merula*) and the amount of damage found on vineyard grapes [22]. However, without evidence of a benefit to the falcons themselves, the effort and cost of translocating individuals of this threatened species to vineyards may be unjustified. Our results show that, within an intensive agricultural area, falcons are capable of feeding their chicks more often and with larger food items, and of spending more time in attendance at the nest, both of which are factors that are associated with increased nesting success [24–25].

In addition to spending more time attending and feeding their chicks, vineyard falcons provided better quality food. They provided significantly more plucked and decapitated prey to their nestlings. By completely removing these indigestible food parts, parents provide chicks with food items that are more energy efficient to digest, and that potentially reduce the risk of ectoparasite exposure to chicks [35]. This behavior may also reduce the chances of attracting predators to the nest by avoiding a buildup of prey remains around the nest area [35].

While the differences observed between habitats in this study may have been due in part to the supplementary food provided to the falcons living in vineyards, removing these feeding events from our models still indicates that falcons living in vineyards are at least as good, if not better, at provisioning nestlings with food as those in the hills. Furthermore, removing the supplementary food from our analysis revealed that falcons in vineyards tend to increase the size of average prey items as chick age increases, whereas those in the hills actually catch smaller prey. Therefore, removing these data provides a highly conservative estimate of differences between the habitat types, as vineyard falcons would likely find other food if supplementary food was unavailable. Further experimentation into the effect of supplementary food on falcons in the vineyards will provide the link necessary to distinguish the quality of the two habitats for falcons. Our results provide evidence that New Zealand falcons are capable of displaying the behavioral plasticity

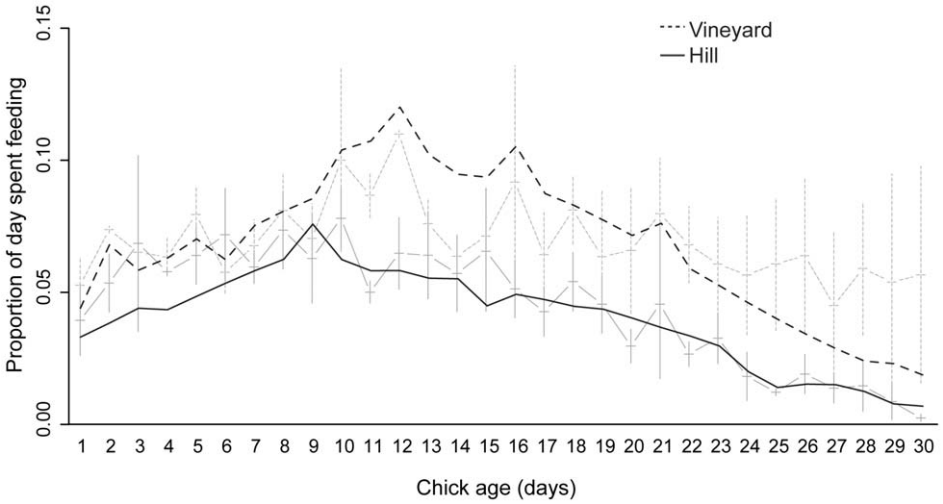

Figure 1. Proportion of the day that parents spent feeding chicks in vineyard and hill nests. Dark lines are the fitted model estimates from a GLMM with a second-order polynomial fitted for chick age. Pale lines are raw data (+/− SEM). Falcons in vineyard nests spent a significantly greater proportion of the day feeding chicks compared with falcons in hill nests ($P<0.05$).
doi:10.1371/journal.pone.0038679.g001

necessary to survive and rear their offspring in a highly altered anthropogenic landscape. This concurs with recent results that suggest that this species is capable of nesting in *Pinus radiata* plantation forestry [27], whereas forestry habitat was previously thought to be deleterious to the falcon [23].

Reproduction is an energetically costly phase in the annual cycle of all breeding birds, and a lack of food over any portion of the reproductive cycle can have limiting effects on both parents and their offspring [36–37]. Nesting birds of prey must balance the relatively low-cost behaviors of caring for their young in the nest (activities such as brooding) with the need to forage away from the nest - a behavior high in metabolic cost. The availability of prey in the areas surrounding the nest therefore has a direct effect on the breeding success of raptors, as is the case with peregrine falcons, *Falco peregrinus*, where increased nest attendance by females is associated with increased nesting success [25]. Providing supplementary food to altricial birds during breeding can therefore positively affect reproduction rates, fledging condition and parent survival [36,38–39]. Similarly, areas of high prey densities are associated with higher reproductive rates [36,38]. In our study area, vineyards have a higher density of avian prey compared with hills [Kross SM, Tylianakis JM, Nelson XJ unpublished manuscript], and falcons were additionally provided with supplementary food. It is therefore difficult to tease out the effect of habitat alone, or supplementary food alone, on nesting falcons. While some other raptors (e.g. kestrels, *Falco tinninculus* [40]) have been shown to benefit from supplementary feeding, our results go further, showing that supplementary feeding alone does not fully explain the positive ramifications that we have demonstrated for vineyard habitat.

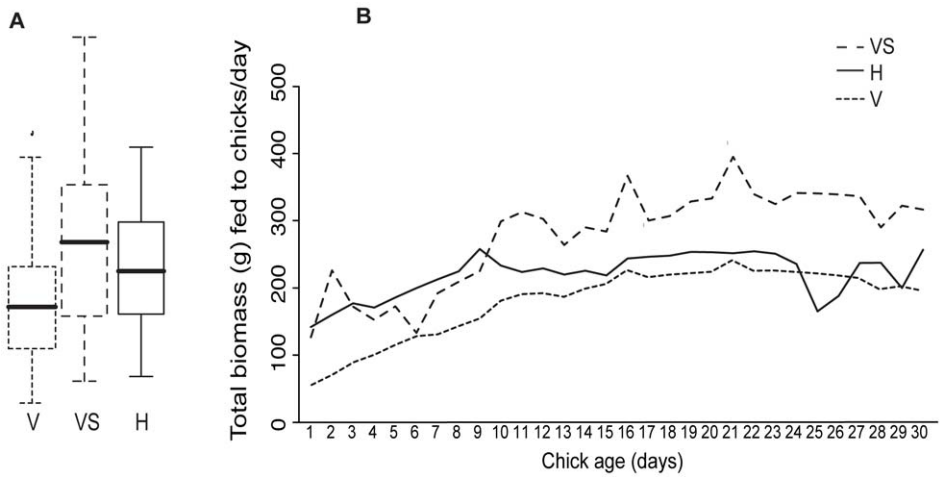

Figure 2. The total biomass of prey brought into nests in vineyards and hills. A The minimum, lower quartile, median, upper quartile, and maximum observations for vineyard nests with supplementary food items excluded (V), for vineyard nests including supplementary food items (VS) and for hill nests (H). **B** The fitted model estimates from a GLMM with a significant second order polynomial fitted for chick age, including supplementary food for vineyard nests (VS) and excluding supplementary food (V) and for hill nests (H). Model estimates indicated that as chick age increased falcons in vineyard nests brought in more total prey each day than did falcons in hill nests ($P<0.001$).
doi:10.1371/journal.pone.0038679.g002

Table 3. Generalized linear mixed effects model coefficients for parental care parameters measured for breeding New Zealand falcons *Falco novaeseelandiae* nesting in managed vineyards and unmanaged hill habitat.

Response variable		Intercept	Effect of habitat (hill nests)	Effect of chick age (per day)	Effect of interaction between habitat and chick age	2 chicks in brood	3 chicks in brood	Quadratic polynomial	Cubic polynomial
Nest attendance (both parents)	Estimate (change from intercept)	0.979	0.946 (−0.033)	0.971 (−0.008)	R	0.992 (0.013)	0.983 (0.004)	0.979 (0.0001)	0.979 (<0.001)
	t-value	12.489	−6.003	−18.516		3.646	1.61	6.062	3.092
	p-value	<0.001	0.005	<0.001		0.027	0.160	<0.001	0.003
Nest attendance (females)	Estimate	0.981	0.953 (−0.03)	0.974 (−0.007)	R	R	R	0.981 (<0.001)	0.981 (<0.001)
	t-value	10.4	−3.006	−17.153				3.014	3.703
	p-value	0.0001	0.02	0.0001				0.004	<0.001
Nest attendance (males)	Estimate	0.0524	0.0858	0.0505	0.0492	R	R	0.0525	0.0524
	t-value	−10.920	1.849	−4.454	−4.056			3.217	1.776
	p-value	<0.001	0.031	<0.001	<0.001			<0.001	0.090
Nest activity (both parents)	Estimate	33.857	26.051	33.046	R	R	R	33.819	R
	z-value	56.30	−4.13	−10.83				−4.34	
	p-value	<0.001	<0.001	<0.001				<0.001	
Brooding rates (both parents)	Estimate	0.9370	R	0.9151 (−0.022)	R	R	R	0.9375 (0.005)	0.9371 (<0.001)
	t-value	10.6		−21.85				10.67	6.21
	p-value	<0.001		<0.001				0.001	0.001
Nest maintenance (both parents)	Estimate	0.0578	R	0.0556 (−0.002)	R	R	R	0.0578	0.0578
	t-value	−32.270		−7.480				2.390	2.740
	p-value	0.0001		0.0001				0.018	0.007

Models for count data were analyzed using Poisson errors, and all other data were logit transformed and modelled using Gaussian errors. Values shown in parentheses under estimates show the change from the model intercept.
R = Predictor variable removed during model simplification.
doi:10.1371/journal.pone.0038679.t003

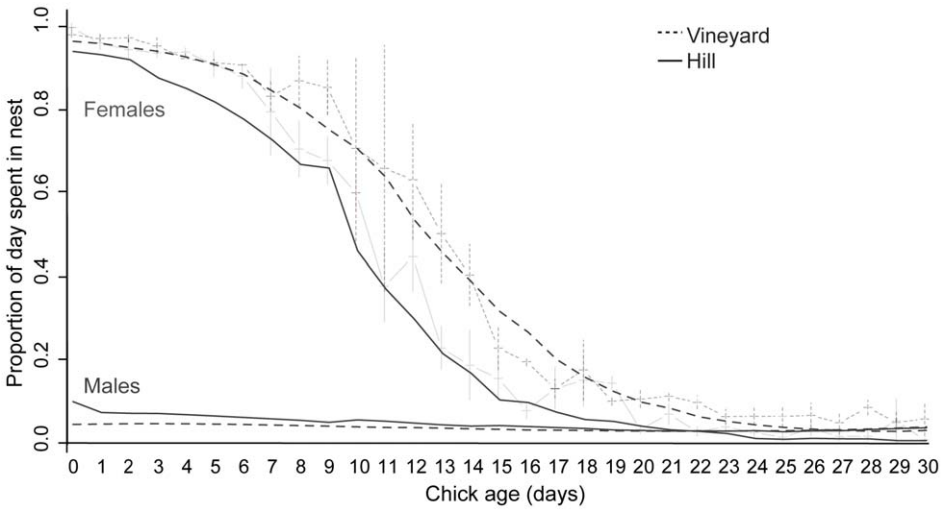

Figure 3. Proportion of the day that both adult falcons were in attendance at the nest as chick age increased in vineyard (dotted lines) and hill (solid lines) nests. Thin grey lines show the raw data for both parents combined, with +SEM for vineyard nests and the data mean – SEM for hill nests. Thick lines show the fitted values from a GLMM including significant second and third order polynomial terms for female falcons (black lines) and from a GLMM including significant second order polynomial terms for male falcons (dark grey lines).
doi:10.1371/journal.pone.0038679.g003

Females were present within the nest for much more of the day than males. Females therefore took on the majority of the nest-based behaviors that were the focus of this study, and it is likely that males took on the majority of foraging, and provisioned females with prey items with which to feed chicks. This most likely occurs because female falcons, as the physically dominant individual in a pair, remain within or near the nest, and intercept males approaching with food in order to feed the chicks themselves, especially prior to chicks being able to thermoregulate, a pattern that has been shown in the peregrine falcon [41]. If males were unable to forage efficiently and females were forced to forage in order to provision chicks, especially when chicks were not yet able to thermoregulate, this could result in lower nesting success. In our study, supplementary food was only relied upon as a food source by one of the vineyard pairs: the remaining 3 pairs used supplementary food for $<10\%$ of their feedings. Interestingly, in these 3 pairs, 98.25% of the supplementary food items were brought to the nest after chicks had reached 14 days of age, by which time adult females had drastically reduced the amount of time they spent in the nest (Figure 3) and were likely to have joined their mates in foraging and food provisioning. Male kestrels have been shown to avoid provisioning their chicks with supplementary food items, whereas females feed both themselves and their chicks with supplementary food when it is available [40], and our results indicate that it is possible this is also the case in New Zealand falcon. Experimentally providing only some of the vineyard falcons with supplementary food in the future will lead to further understanding of the effect of habitat alone in the breeding behavior of the threatened New Zealand falcon.

Parents in nests with more chicks fed their chicks a greater total biomass per day, and fed them more often. However, these increases did not fully compensate for the sharing of food items amongst chicks. On average, single chicks received more food per day (174 g), than each of two chicks (131 g) or three chicks (97 g), and this effect remained even after removing supplementary food from the analysis. These results indicate that removing chicks from hill nests (as carried out by the FFG project) may benefit the remaining chick through increased food provisioning. However, this assumption does not take into account the behavioral impact of removing siblings on the remaining chick [42], or the impact of this harvest of individuals on the falcon population in the hills [18].

One important caveat to the conservation implications of this study is mortality as a consequence of electrocution, which may increase due to the prevalence of power lines in anthropogenic habitats. There is some evidence [43] to suggest that falcons residing in vineyards are suffering significant losses due to electrocution, a common pattern among raptors [5]. However, it has recently been demonstrated that if political will can be found, initiatives to mitigate these effects are both effective and affordable [7].

Our results suggest that there is considerable potential in the idea of reintroducing falcons into vineyards. We have previously demonstrated significant economic benefits for vineyards containing falcons due to a reduction in damaged or destroyed grapes [22]. Here, we showed that there may also be beneficial effects for falcons breeding within vineyards, as falcons in vineyards had higher nest attendance, spent more time feeding chicks, and fed chicks more often and with more food compared with falcons in hill nests.

Supporting Information

Table S1 Explanation of nest disturbance scores.
(DOC)

Acknowledgments

We thank A. Stow and 2 anonymous reviewers for providing constructive reviews of a previous draft of this manuscript. For advice, assistance with locating nests and placing cameras we thank: C. Wynn, N. Fox, H. Oliver, L. Olley, P. Lintott, J. Cooper, J. Crowe, B. Coles, J. Knott, J. Kumagai, K. Morgan, X. Birch, R. Seaton, D. Harliwich and E. Soper. For access to land, we thank: Nelson Forests Ltd (D. Parsons), Winegrowers of ARA, Marisco Vineyards (R. Clare), M. Gifford, Spray Point Station (J & R Mapp), Richmond Brook Station, Wye Hills Farm (E & J Rentoul), as well as all landowners who provided access for falcon nest searches. E. Soper & R. Homewood provided assistance with video scoring and Pernod Ricard NZ (C. Monk) provided electrical assistance. Permits and advice for this

research were supported by P. Gaze and the Department of Conservation (NM-23677-FAU) and ethics permission was provided by the University of Canterbury (2008/27R).

Author Contributions

Conceived and designed the experiments: SMK JMT XJN. Performed the experiments: SMK. Analyzed the data: SMK JMT XJN. Wrote the paper: SMK JMT XJN.

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APPENDIX SIX

ASSAB CONFERENCE POSTER

This poster was presented at the April 2009 conference of the Australasian Society for the Study of Animal Behaviour at Massey University in Auckland, New Zealand. It was awarded the prize for "*Best Poster by a Student*".

Observing New Zealand falcon nests using remote videography

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The New Zealand falcon is chronically threatened and is New Zealand's only endemic diurnal raptor. Since 2005, as part of a conservation programme, falcon nestlings have been relocated from nests in the arid hills of Marlborough into artificial nests in the vineyard-dominated landscape of the Wairau valley. There is a small population of falcons now breeding in the vineyards. As part of a PhD study examining the behavioural differences between the 'hills' and 'vineyard' population of falcons, we are using remote videography to compare the nestling diets, prey delivery rates, and nesting behaviours of the two falcon populations. Details of the remote videography technology will be discussed, along with recommendations for future use of this methodology for studying New Zealand falcons.

The Use of Remote Videography to Observe the Nesting Behaviour of New Zealand Falcons

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Why We Came

As part of a PhD project examining the behavioural changes elicited in New Zealand falcons as a result of being moved from their natural habitats and relocated into a vineyard-dominated landscape, we have begun collecting data on the nesting behaviour displayed by falcons within the two habitats.

Compared with the more traditional methods of collecting prey remains and pellets, remote videography (nest cameras) is a more effective means of assessing raptor diet during the breeding season. (Lewis et al. 2004).

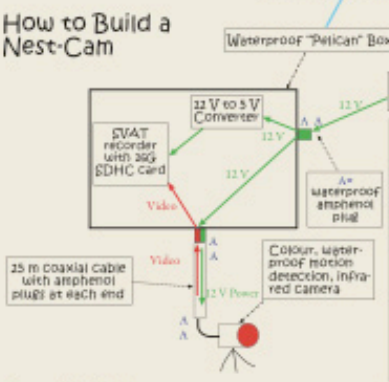
This method is especially suitable when considering New Zealand falcons, which digest virtually all prey bones and feathers, leaving little discernable remains in the form of pellets (Fox 1977).

What We Did

The design for the nest cameras was based on a set-up used by the Department of Conservation. By adding a solar panel to the design, and using Secure Digital High Capacity (SDHC) cards we were able to increase the amount of time required between visits to download video and change batteries.

- Camera placed in position with best view of chicks while remaining unobtrusive to falcon activities
- Battery and SDHC card changed every 4 days
- Portable DVD player used to check that the system was working properly
- Digital video can be viewed in fast-forward, or slowed to frame-by-frame to identify prey

How to Build a Nest-Cam



Setting up the nest camera

What We Saw

Preliminary review of ten days of video from one of the five nests revealed emerging patterns pertaining to feeding rates. A full review of the remaining 144 days of video may confirm these patterns and should reveal further information about the nesting habits and prey preferences of falcons.

Fig. 1 Mean biomass per prey item compared with mean length of feeding events per day.

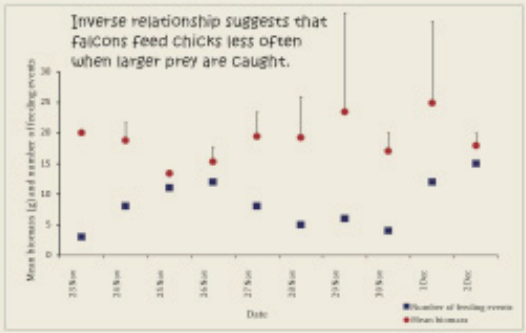


Fig. 2 Mean biomass per prey item compared with number of feeding events per day.

A complete recording of a feral cat predating a nest was obtained, confirming that feral cats are predators of falcon nests.

The cat returned over two nights to kill all three 29-day-old chicks.

A common gecko was brought to the nest by the male falcon.

This is a previously unknown prey species for New Zealand falcons.

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Acknowledgements

UC supplied the equipment for nest cameras. Craig Morley, Mandy and Bernard Kross, NZ Department of Conservation, Dr. Lesley Boyd, Dept. of Anthropology, Otago University, Dr. Jolie Gabet, Colin Wynn, Paul Lawson, James Dyson & Kate Morgan for helping with camera installations. Thank you to all the landowners who gave us access to their property.

Candid Camera

Mrs Falcon with dinner: an adult male yellowhammer

Mr Falcon feeding 15 day old nestlings

Mrs Falcon with a large meal: a rabbit

The nestlings wait for mum to tear up their meal

As they get older, the nestlings compete for food

Nestlings at 27 days are almost as big as the adults